ARCHOSAUR EVOLUTION DURING THE JURASSIC: A SOUTHERN PERSPECTIVE

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ABSTRACT

The fossil record of archosaurs - crocodylomorphs, pterosaurs and dinosaurs - from the Jurassic of the Southern Hemisphere is critically reviewed, and its evolutionary implications are evaluated. Although several important faunas and also isolated finds are known from Gondwana, the record in total is still very patchy, and any evolutionary scenario based on this record should be seen as tentative. Compared to the Northern Hemisphere, southern archosaurs are much more poorly known, which is especially true for terrestrial crocodiles and pterosaurs. Marine crocodiles are rather well represented in south-western South America, whereas the report of terrestrial archosaurs is currently best for Africa. However, in South America, important and especially promising archosaur faunas are known from the Callovian Cañadón Asfalto and the (?)Tithonian Cañadón Calcáreo formations of Chubut province, Argentina. Early and Middle Jurassic Gondwanan archosaurs demonstrate that the faunas of that period still had a generally Pangean distribution, whereas first indications of differential archosaur evolution in the Northern and Southern Hemispheres are evident in Late Jurassic Gondwanan faunas.

Keywords: *Crocodylomorphs, Pterosaurs, Dinosaurs, Gondwana, Fossil record*

RESUMEN: *La evolución de los arcosaurios durante el Jurásico: una perspectiva desde el Sur.* El presente trabajo incluye una revisión crítica del registro fósil de los arcosaurios - cocodrilos, pterosaurios y dinosaurios - del Jurásico del Hemisferio Sur. Se evalúan además, sus implicancias evolutivas. Aunque se conocen varias faunas importantes y hallazgos aislados, el registro, en su totalidad, es todavía incompleto y cualquier escenario evolutivo basado en este registro debería verse como tentativo. En comparación con la situación en el Hemisferio Norte, es mucho menos lo que sabemos sobre los arcosaurios del Hemisferio Sur, y esto es especialmente cierto para los cocodrilos terrestres y pterosaurios. Los cocodrilos marinos están bastante bien representados en el sudoeste de Sudamérica, en tanto que el registro de arcosaruios terrestres es actualmente mejor en África. No obstante, en Sudamérica, se conocen faunas importantes, y especialmente prometedoras, del Caloviano de la Formación Cañadón Asfalto y del Titoniano (?) de la Formación Cañadón Calcáreo, en la provincia de Chubut, Argentina. Las faunas de arcosaurios del Jurásico Temprano y Medio de Gondwana muestran una distribución pangeica, en tanto que los primeros indicios de diferenciación en la evolución de los arcosaurios de los Hemisferios Norte y Sur se evidencian en las faunas gondwánicas del Jurásico Tardío.

Palabras clave: *Cocodrilos, Pterosaurios, Dinosaurios, Gondwana, Registro fósil*

INTRODUCTION

Archosaurs - crocodylomorphs, pterosaurs, dinosaurs, and several basal, mainly Triassic groups - are certainly one of the most prolific clades of Mesozoic terrestrial vertebrates, and their living representatives, modern crocodiles and birds, are important components of recent vertebrate faunas. All three derived groups (crocodylomorphs, pterosaur, dinosaurs) originated in the later stages of the Triassic, but experienced their first and most important radiations in the Jurassic. In crocodylomorphs, the Jurassic saw the origin and diversification of the Mesoeucrocodylia, the largest clade, which also includes the modern forms (Fig. 1, *e.g.* Benton and Clark 1988, Tykoski *et al.* 2002, Pol and Gasparini 2007). In pterosaurs, the early "rhamphorhynchoid" faunas reached their peak diversity during this period, and the pterydactyloids, to which almost all Cretaceous pterosaurs belong, originated and first diversified in the Upper Jurassic (Fig. 2, Kellner 2003, Unwin 2003, 2006). Dinosaurs started with only a few clades into the Jurassic, almost none of which survived this period. However, by the end of this period, basically all important lineages were established (Fig. 3, Sereno 1999a, Weishampel *et al.* 2004). The Jurassic thus witnessed important faunal turnovers in all major clades of archosaurs and is therefore of greatest importance for our understanding of the evolutionary history of these groups.

It is still rather unclear what caused these important changes in Jurassic archosaur faunas. In the Jurassic the initial break-up of the supercontinent of Pangea took

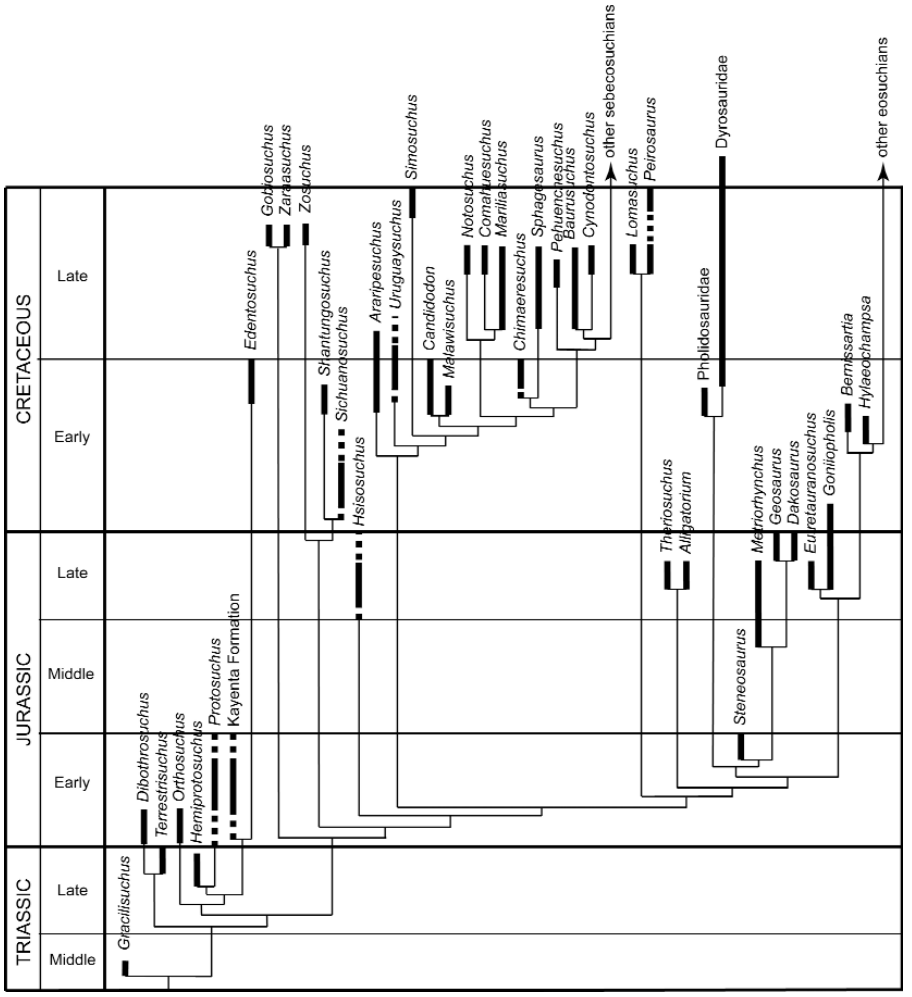

Figure 1: Phylogeny of crocodiles showing the origin and first diversification of the Mesoeucrocodylia during the Jurassic. Based on Pol and Gasparini (2007). Dotted lines indicate uncertain limits of the stratigraphic range of the bearing sediments of a certain taxon.

place, during which the western Tethian and northern Atlantic oceans opened and finally separated Gondwana from the northern continents in the Late Jurassic (Scotese 1991, Smith *et al.* 1994, Scotese *et al.* 1999, Ford and Golonka 2003). Vicariance as a consequence of this separation has been proposed as an important aspect of dinosaurian radiations (Russell 1993, Sereno 1999a, b), and evidence for continent-wide vicariance was found in empirical analyses of dinosaurian biogeography (Upchurch *et al.* 2002). Furthermore, these changes in geography brought about other modifications, such as the end of the megamonsoonal climate that had dominated large parts of Pangea in the Triassic and early stages of the Jurassic (Parrish 1993, Scotese *et al.* 1999). Archosaur radiations and faunal turnovers certainly have to be seen in the context of these environmental changes (see Forster 1999), but even the timing and the modes of these evolutionary events are still largely unknown, owing to the rather poor Jurassic fossil record in many groups. Furthermore, our current ideas about Jurassic faunal changes are almost entirely based on the fossil record of the Northern Hemisphere, making it basically impossible to check possible effects of the separation of Gondwana on the evolutionary history of the different groups.

In the current paper, we critically evaluate the Jurassic archosaur fossil record of the Southern Hemisphere and its importance for our current understanding of Jurassic archosaur evolution. In the following, the colloquial term "crocodile" is used to refer to crocodylomorphs in general. True members of the Crocodylia are so far unknown from the Jurassic and only appear in the Cretaceous.

Institutional abbreviations: MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, MB: Museum für Naturkunde, Berlin, MPEF: Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

JURASSIC ARCHOSAURS FROM THE SOUTHERN HEMISPHERE

Jurassic terrestrial archosaurs from the Southern Hemisphere are known only from a handful of localities (Fig. 4), and most finds are isolated and/or fragmentary. In the following, the Gondwanan archosaur fossil record will be briefly outlined and compared with that from the Northern Hemisphere. Only the body fossil record will be dealt with in detail here. Although tracks can give important insights into faunal compositions and other aspects of archosaur biology, they are usually less diagnostic than body fossils on a lower taxonomic level. Thus, the, for some stages, more numerous track record is only taken into consideration in cases where it inidcates the presence of otherwise not represented groups.

Early Jurassic

The Early Jurassic Gondwanan archosaur record is strongly biased towards Africa, with one important fauna known from India, and isolated occurrences from South America and Antarctica (Fig. 4a).

The most important Lower Jurassic Gondwanan vertebrate faunas are certainly those of the Upper Karoo Supergroup, namely the upper Stormberg Group, comprising the Upper Elliot and Clarens formations [Fig. 4a (1), see Knoll 2005], and contemporaneous units in

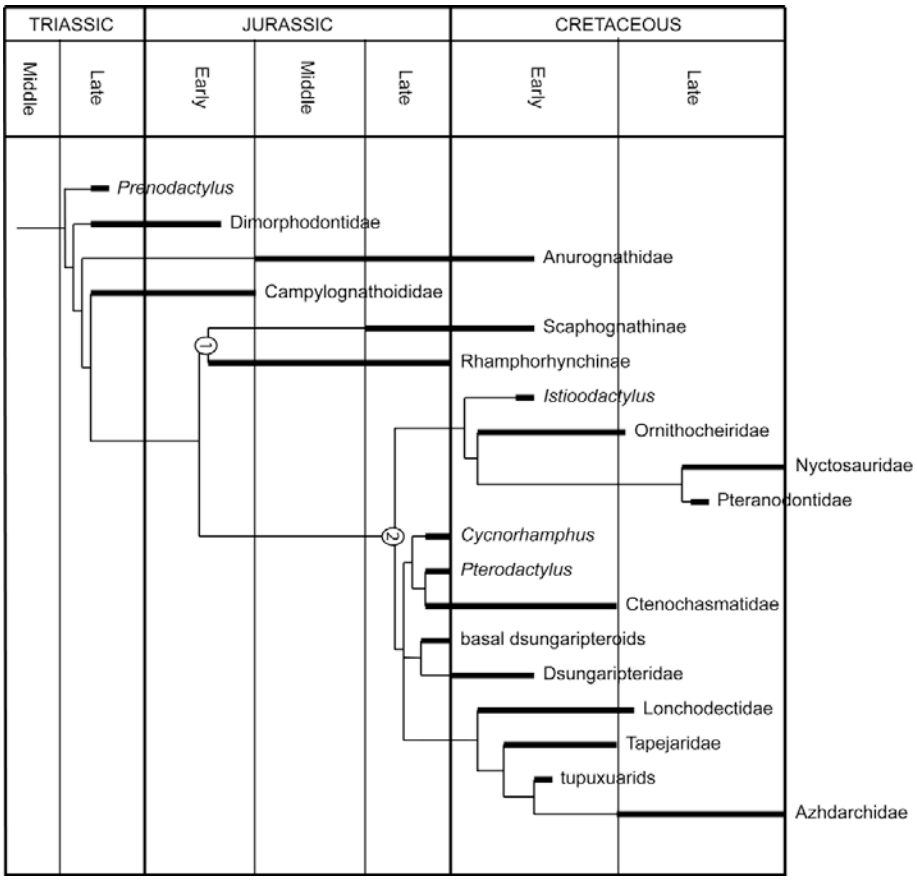

Figure 2: Phylogeny of pterosaurs showing the origin and first diversification of the two main lineages, Ramphorhynchidae (node 1) and the Pterodactyloidea (node 2) during the Jurassic (based on Unwin 2006).

Zimbabwe, such as the Forest Sandstone. Several taxa of crocodylomorphs have been described especially from the Upper Elliot and Clarens formations, but many of them seem to be junior subjective synonyms of other taxa (see review in Knoll 2005). Taxa currently regarded as valid (Knoll 2005) include the 'sphenosuchians' *Sphenosuchus* (Haughton 1915, Walker 1990) and *Litargosuchus* (Clark and Sues 2002), and the protosuchids *Protosuchus* (Gow 2000) and *Orthosuchus* (Nash 1968, Pol *et al.* 2004). Pterosaur remains are currently unknown from the Elliot and Clarens Formations, though this group might be represented by tracks (Knoll 2005).

Dinosaurs are certainly the best-represented and best-known archosaur group from the upper Stormberg Group and equivalent strata in southern Africa (South Africa, Lesotho and Zimbabwe). Since the first description of the "prosauropod" *Massospondylus* from the Upper Elliot Formation by Owen (1854), a plethora of dinosaurs, mainly basal sauropodomorphs, have been described from these units. However, most of these taxa are considered to be junior synonyms of *Massospondylus* (Cooper 1981), which remains the best known Early Jurassic "prosauropod" from the Southern Hemisphere, and is well-documented from the upper Stormberg (*e.g.* Gow 1990, Gow *et al.* 1990, Sues *et al.* 2004, Yates and Vasconcelos 2005, Barrett and Yates 2006), including remains of eggs and embryos (Reisz *et al.* 2005), but also known from other Early Jurassic units in southern Africa, mainly Zimbabwe (Cooper 1981). However, although *Massospondylus* certainly represents the most common sauropodomorph in the upper Stormberg, at least one other "prosauropod" and two basal sauropods are also present in this unit (Barrett 2004, Yates *et al.* 2004, 2007), and the basal sauropod *Vulcanodon* has been described from strata of Early Jurassic age in Zimbabwe (Raath 1972, Cooper 1984). Theropod dinosaurs from the Early Jurassic of southern Africa include the small coelophysoid *Coelo-physis rhodesiensis*, which represents one of the best-known Early Jurassic theropods (Raath 1969, 1977, 1985, 1990, Galton 1971, Chinsamy 1990, Bristowe and Ra-ath 2004). Most material of this theropod comes from the Forest Sandstone of Zimbabwe (Raath 1969, 1977), but the taxon also seems to be represented in the Upper Elliot Formation (Raath 1980). Recently, Yates (2005) described a new taxon of theropod from the Upper Elliot Formation, *Dracovenator*. Recent fieldwork indicates, however, that this specimen might be derived from the basal part of the overlying Clarens Formation (OR, pers. obs. 2008).

The Upper Elliot Formation has yielded the most diverse Early Jurassic ornithischian fauna known. Taxa represented include the heterodontosaurids *Heterodontosaurus*, *Lycorhinus* and *Abrictosaurus* (Haughton 1924, Crompton and Charig 1962, Hopson 1975, see also Knoll 2005), the probably basal thyreophoran *Lesothosaurus* (Thulborn 1970, 1972, Galton 1978, Sereno 1991, Butler *et al.* 2008), and the basal cerapodan *Stormbergia* (Knoll 2002a, b, Butler 2005).

Apart from the Karoo basin, Early Jurassic archosaurs from Africa have only been described from Morocco [Fig. 4a (2)]. Material from the Toundoute continental series of the High Atlas include the basal sauropod *Tazoudasaurus* (Allain *et al.* 2004) and the probable abelisauroid theropod *Berberosaurus* (Allain *et al.* 2007). Furthermore, Taquet (1985) reported and figured a partial theropod hindlimb from an unnamed Early Jurassic unit in Morocco.

Outside Africa, the most important Early

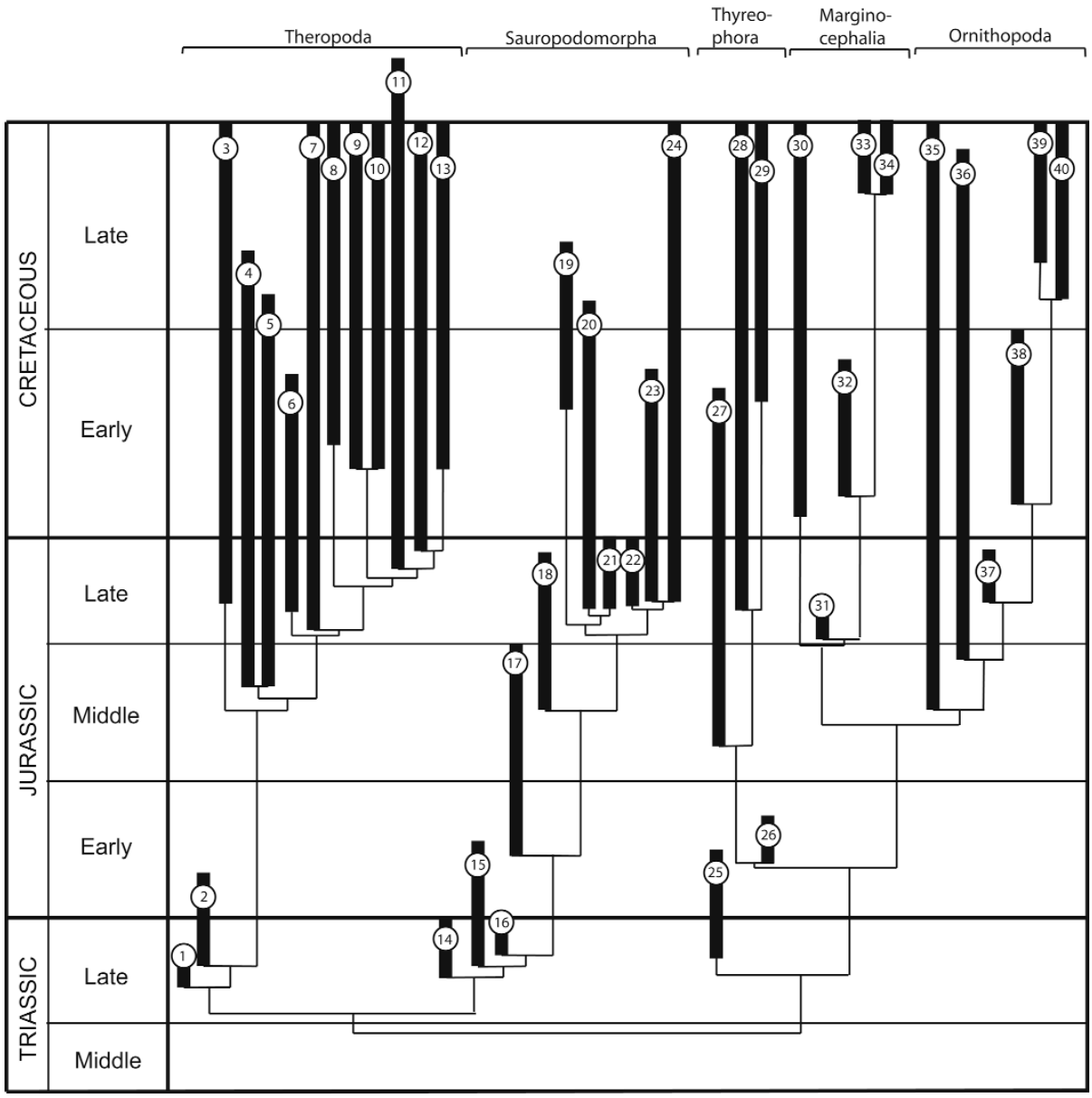

Figure 3: Phylogenetic relationships and stratigraphic distribution of the main dinosaur clades, showing the diversification of almost all main dinosaur lineages during the Jurassic. Minor clades or single taxa have been considered if of stratigraphic importance. Composite cladogram, Theropoda (based on Rauhut 2003), Sauropodomorpha on Wilson (2002) and Smith and Pol (2007), and Ornithischia on Weishampel, Dodson and Osmólska (2004) and Butler *et al.* (2008). 1) Herrerasauridae, 2) Coelophysoidea, 3) Ceratosauria, 4) Allosauroidea, 5) Spinosauroidea, 6) Coeluridae, 7) Tyrannosauroidea, 8) Ornithomimosauria, 9) Oviraptorosauria, 10) Therizinosauroidea, 11) Avialae, 12) Dromaeosauridae, 13) Troodontidae, 14) Plateosauridae, 15) Massospondylidae, 16) *Antetonitrus* + *Lessemsaurus*, 17) Cetiosauridae (sensu Upchurch *et al.* 2004), 18) Omeisauridae, 19) Rebbachisauridae, 20) Dicraeosauridae, 21) Diplodocidae, 22) *Camarasaurus* spp., 23) Brachiosauridae, 24) Titanosauria, 25) Heterodontosauridae, 26) *Emausaurus,* 27) Stegosauria, 28) Ankylosauridae, 29) Nodosauridae, 30) Pachycephalosauria, 31) Yinlong, 32) Psittacosauridae, 33) Centrosaurinae, 34) Chasmosaurinae, 35) "Hypsilophodontidae" (non-monophyletic group of basal ornithopods, the interrelationships of which are still unclear), 36) Dryosauridae, 37) *Camptosaurus* spp., 38) Iguanodontidae, 39) Hadrosaurinae, 40) Lambeosaurinae.

Jurassic Gondwanan archosaur localities are found in the Prahita-Godavari valley of eastern India, mainly from the Kota Formation [Fig. 4a(3)]. However, it might be noted that, although the Kota Formation is generally considered to be Early Jurassic in age (Bandyopadhyay *et al.* 2002, Weishampel *et al.* 2004, Bandyopadhyay and Sengupta 2006), there is some uncertainty about the dating of this unit, and it might be as young as Early Cretaceous (Prasad *et al.* 2004, Prasad and Manhas 2007).

Again, it was Owen (1854) who first reported archosaur remains from this area, from levels now assigned to the Kota Formation. The remains described by Owen (1854) represent a marine, thalat-

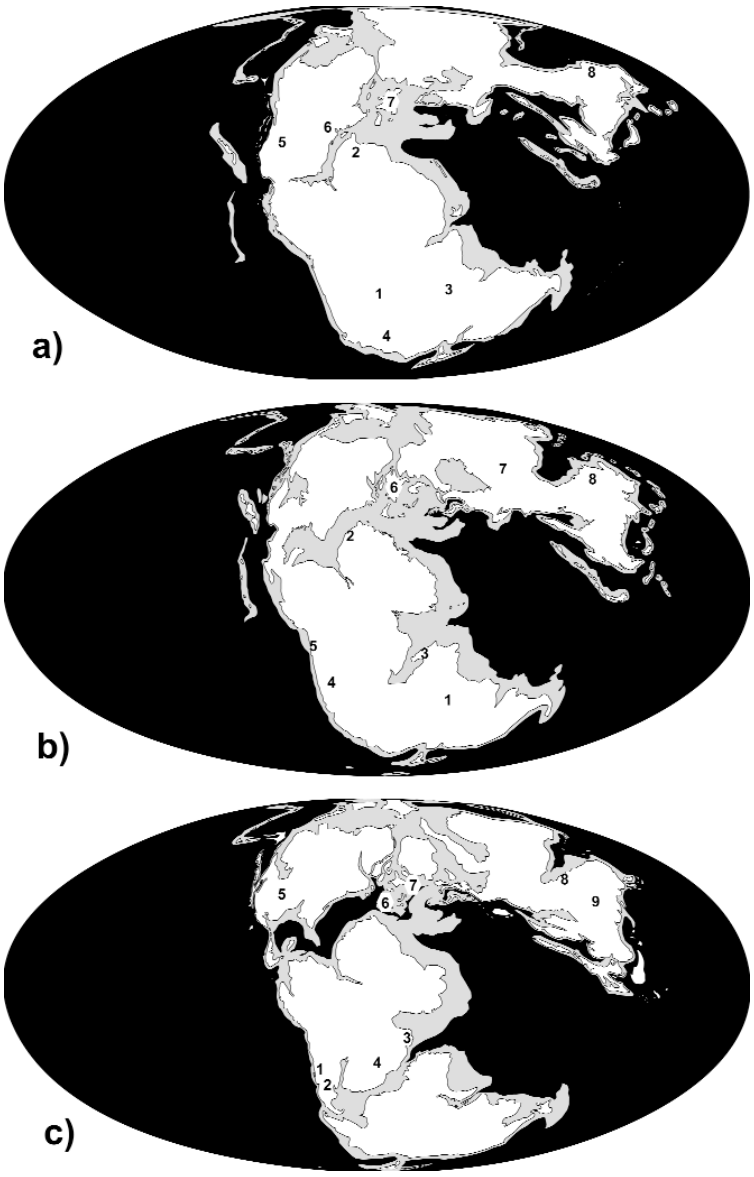

Figure 4: Palaeogeographic maps (modified from Mollewide Plate Tectonic Maps available at http://jan.ucc.nau.edu/~rcb7/globaltext2.html) indicating the main Jurassic archosaur localities in Laurasia and Gondwana. a) Early Jurassic: Elliot and Clarens formations, upper Stormberg Group, Upper Karoo Supergroup, South Africa (1), Toundoute continental series, High Atlas, Morocco (2), Kota Formation, Prahita-Godavari valley, India (3), Hanson Formation, Transantarctic Mountains, Antarctica (4), Kayenta Formation and Navajo Sandstone and equivalent beds, USA (5), Newark Supergroup, North America (6), Posidonia Shale in Germany and comparable strata in England and France (7), Lufeng Formation, China (8). b) Middle Jurassic: Durham Downs, Queensland, Australia (1), Tilougguit Formation and equivalent beds of Morocco (2), Isalo III Formation, Madagascar (3), Cañadón Asfalto Formation, Chubut, Argentina (4), Lautaro Formation, Chile (5), various marine localities in England and France (6), Balabansai Formation, Kirghizia (7), Lower Shaximiao Formation, Sichuan, China (8). C. Late Jurassic: Vaca Muerta Formation and equivalent beds, Neuquén Basin, Argentina (1), Cañadón Calcáreo Formation, Chubut, Argentina (2): Tendaguru Beds, Tanzania (3), Kadsi Formation, Zimbabwe (4), Morrison Formation, USA (5), various localities in Portugal (6), Solnhofen Limestone and equivalent beds in Germany (7), Shishougou Formation, Xinjiang, China (8), Upper Shaximiao Formation of China (9).

tosuchian crocodile (Kutty *et al.* 1987, Bandyopadhyay *et al.* 2002), and are still the only crocodile remains described from the Gondwana sequence of this basin. However, it might be noted that a partial skull from the Lower Jurassic Kota Formation of India, referred to an ankylosaurian dinosaur by Nath *et al.* (2002: pl. 1a-e), most probably represents a crocodilian, as indicated by the pitted bone surface and the general shape of the fragments. Judged by the general morphology, this fragment most probably represents a terrestrial crocodile, but further interpretation has to await a detailed reanalysis of this specimen.

Jain (1974) described the campylognathoid pterosaur *Campylognathoides indicus* from the upper levels of the Kota Formation, which still represents the oldest pterosaur known from the Southern Hemisphere. Dinosaurs from the Kota Formation were described by Jain *et al.* (1975, 1979) and Yadagiri (1988, 2001), who named and described the sauropods *Barapasaurus* and *Kotasaurus*, respectively. The material referred to the latter taxon includes at least one further taxon of sauropod (OR, pers. obs. 2005). Nath *et al.* (2002) described fragmentary dinosaur remains from the Kota Formation and referred them to an ankylosaurian thyreophoran, which would represent the oldest record of this group. However, this identification is questionable, since more than one taxon is represented in the material (see comments on a probable crocodylomorph included in this material above), but some of the scutes described and figured by Nath (2002: pl. 1f-j) might indeed represent a thyreophoran. Apart from these remains, theropods are represented in the Kota Formation by undiagnostic material (Bandyopadhyay *et al.* 2002, Prasad and Manhas 2007).

Just recently, Kutty *et al.* (2007) described two taxa of sauropodomorphs, the "prosauropod" *Pradhania* and the probable basal sauropod *Lamplughasaura*, and mentioned the presence of a third sauropodomorph taxon in the Upper Dharmaran Formation (Sinemurian), which underlies the Kota Formation.

Bradmeister *et al.* (2006) described a vertebrate fauna, including probable theropod and sauropod teeth, from the Isalo II Formation of Madagascar. Although

they stated in the abstract that the vertebrate fauna indicates an Early Jurassic age for this fauna, the faunal association, including probable colobodontid fishes and aetosaurian and phytosaurian archosaurs, is more indicative of a Late Triassic age.

Only fragmentary archosaur material has been described from the Early Jurassic of South America so far. Huene (1927) described Lower Jurassic crocodile remains from Mendoza province in Argentina, South America. The material consists of two dorsal vertebrae, which he made the type of a new species of the thalattosuchian *Steneosaurus*, *Steneosaurus gerthi*, but this species is currently considered to be a *nomen dubium* (Pol and Gasparini 2007). An articulated partial metatarsus from the Sinemurian of Alto de Varas in the Cordillera de Domeyko in Chile was described by Chong-Diaz and Gasparini (1972) and also referred to a thalattosuchian (see also Gasparini 1985, Gasparini *et al.* 2000). Early Jurassic dinosaur remains have been described from the probably Lower Jurassic La Quinta Formation of Venezuela. Russell *et al.* (1992) and Sánchez-Villagra and Clark (1994) reported ornithischian material from this formation, which they referred to the southern African genus *Lesothosaurus*, and Moody (1997) described some unidentifiable theropod teeth. However, a recent revision of this material shows that the ornithischian material is not referable to *Lesothosaurus*, and that a further taxon of probable basal saurischian was present (Barrett *et al.* 2008). Martínez (1999) referred some material from the probably Early Jurassic Cañón de Colorado Formation of the province of San Juan, Argentina, to *Massospondylus*, though reexamination of this material indicates that it represents a new genus (Pol, pers. com. 2008). Another basal sauropodomorph has recently been reported from the Las Leoneras Formation of the province of Chubut, Argentina (Pol and Garrido 2007), but these remains have not been described in detail yet.

A noteworthy Early Jurassic vertebrate fauna, including dinosaurs, from Hanson Formation in the Transantarctic Mountains of Antarctica [Fig. 4a(4)] was made known by Hammer and Hickerson (1994). This southernmost archosaur fauna discovered so far includes a humerus of a pterosaur, the theropod *Cryolophosaurus*, the basal sauropodomorph *Glacialisaurus*, and an undescribed sauropod (Hammer and Hickerson 1994, 1999, Smith and Pol 2007, Smith *et al.* 2007a, b).

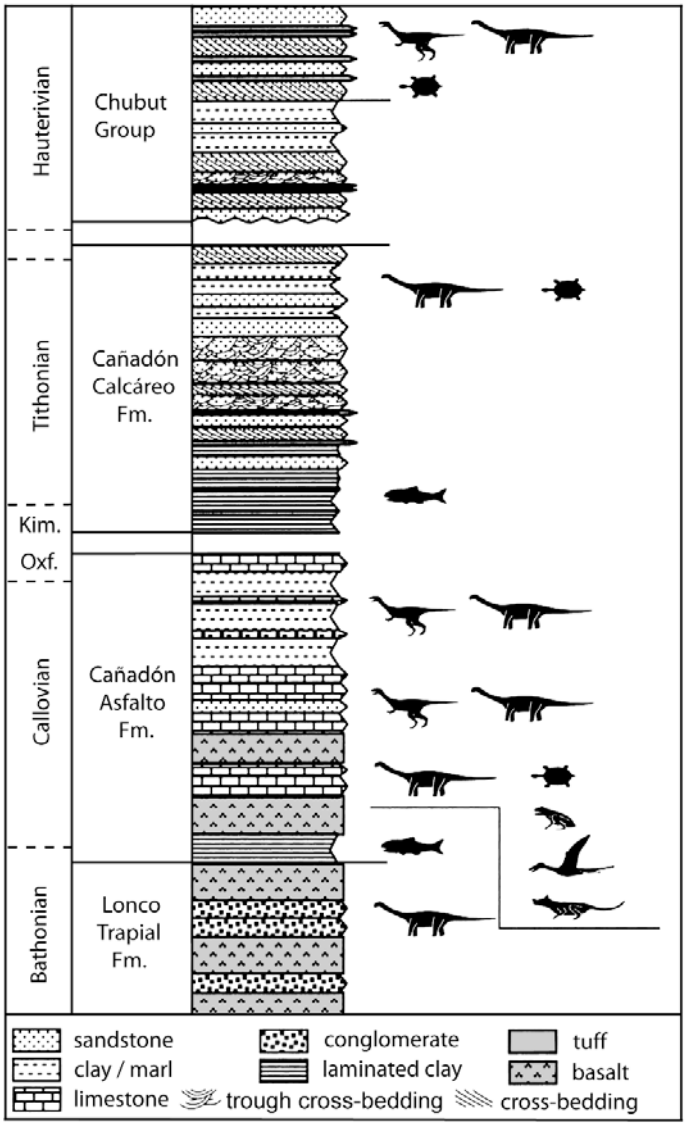

Figure 5: Schematic stratigraphic column of the archosaur-bearing units of the Middle Jurassic Cañadón Asfalto Formation and the Late Jurassic Cañadón Calcáreo Formation of Chubut province, Argentina.

Middle Jurassic

From Australia, only a distal theropod tibia and some fragmentary sauropod remains of Middle Jurassic age have been reported so far, and were named *Ozraptor* and *Rhoetosaurus*, respectively (Longman 1926, 1927, Long & Molnar 1998). *Ozraptor* comes from the shallow marine Colalura Sandstone (Bajocian) of western Australia, whereas *Rhoetosaurus* was found in terrestrial deposits at Durham Downs in Queensland [Fig. 4b(1)].

Middle Jurassic strata in Africa have yielded a few dinosaur remains from the Bathonian-Callovian Tilougguit Formation and equivalent beds of Morocco [Fig. 4b (2)], including the sauropods *"Cetiosaurus" mogrebiensis* and *Atlasaurus imelakei* (Lapparent 1955, Monbaron *et al.* 1999), as well as the sauropod *Chebsaurus algerien-*

sis from indeterminate Middle Jurassic rocks of Algeria (Mahammed *et al.* 2005). Isolated vertebrae from the Bathonian of Morocco that were originally described as a theropod, *Megalosaurus mersensis*, by Lapparent (1955), probably represent a thalattosuchian crocodile (Chabli 1985). However, theropods are represented in the Bathonian of Morocco by isolated and unidentified teeth (Monbaron *et al.* 1999). Remains of the thalattosuchian *Steneosaurus* are found in the Bathonian of Tunisia (Mueller-Töwe 2006).

The Bathonian Isalo III Formation of Madagascar [Fig. 4b(3)] has yielded a rich, though mainly fragmentary archosaur fauna. Taxa reported include a possible atoposaurid crocodilian, a "rhamphorhynchoid" pterosaur, indeterminate ornithischians, theropods, all represented by teeth only (Flynn *et al.* 2006), and the sauropods *Lapparentosaurus madagascariensis* and *Archaeodontosaurus descouensi* (Bonaparte 1986a, Buffetaut 2005, Maganuco *et al.* 2005). Flynn *et al.* (2006) also listed the sauropod species *Bothriospondylus madagascariensis* in the Isalo III Formation, but the material of this taxon was referred to the new genus *Lapparentosaurus* by Bonaparte (1986a, see also Buffetaut 2005), and furthermore referred several teeth to an unspecified neosauropod, though they noted that the apparent differences to the teeth of *Archaeodontosaurus* might be due to preservation, so this assignment is questionable. Thus, only two sauropod taxa are recognized from this formation, *Lapparentosaurus* and *Archaeodontosaurus*. Maganuco *et al.* (2005) referred theropod teeth to several different groups of theropods, including advanced coelurosaurs, but Flynn *et al.* (2006) considered all this material as Theropoda indet. In addition to the fauna from the Isalo III Formation, material of the thalattosuchian *Steneosaurus* has been reported from the Callovian of Madagascar (Mueller-Töwe 2006).

Middle Jurassic archosaurs from South America are mainly known as isolated finds, with the exception of the fauna from the Cañadón Asfalto Formation of Chubut, Argentina [Figs. 4b(4), 5]. This Callovian unit has yielded so far unidentified and unstudied crocodile remains, as well as a diverse, but also still unstudied pterosaur fauna, comprising at least three taxa, possibly including the oldest pterodactyloid known from Gondwana (Rauhut *et al.* 2001, Unwin *et al.* 2004, Rauhut, unpublished data). Most of the remains come from a single pterosaur bonebed, which has yielded disarticulated, but very well-preserved and three-dimensional material (Fig. 6), which is very rare in Jurassic pterosaurs, potentially making this the most important Middle Jurassic pterosaur locality globally. Most noteworthy, however, is the dinosaur fauna, which is the second most diverse Middle Jurassic dinosaur fauna known, following the Bathonian Laurasian fauna from the Lower Shaximiao Formation of China (Peng *et al.* 2005). Taxa described include the sauropod *Patagosaurus* and *Volkheimeria,* and the theropods *Piatnitzkysaurus* and *Condorraptor* (Bonaparte 1979, 1986b, Rauhut 2005a), and at least one further taxon of sauropod is present (Rauhut 2003a). Ornithischian dinosaurs have not been described from this formation so far, but are represented by an isolated ungual from the locality of Cerro Cóndor (Fig. 7) and some teeth from the microvertebrate locality Queso Rallado.

Apart from the fauna of the Cañadón Asfalto Formation, the most important archosaur remains from South America are marine crocodiles from western Argentina and Chile, which include the oldest record of the genus *Metriorhynchus* from the Bajocian Lautaro Formation of Chile [Fig. 4b(5), Gasparini *et al.* 2000]. Two species of *Metriorhynchus* were described from the Callovian of Chile, *Metriorhynchus casamiquelai* from an unnamed unit in the Quebrada Sajasa in northern Chile (Gasparini and Chong Díaz 1977, Gasparini 1985), and *Metriorhynchus westermanni* from the Mina Chica For-mation of northern Chile (Gasparini 1980, 1985) [Fig. 4b(5)]. The latter was regarded as a synonym of the former by Gasparini *et al.* (2000), but new material shows that it is a valid taxon (Gasparini *et al.* in press). Further thalattosuchian oc-currences in Chile were discussed by Gasparini *et al.* (2000). Recently, Gaspa-rini *et al.* (2005) reported a fragmentary skull of *Metriorhynchus* from the Batho-nian of the Los Molles Formation of Neuquén province, Argentina.

Apart from the fauna of the Cañadón Asfalto Formation, Middle Jurassic dinosaurs from South America are only known from two localities in Argentina. Cabrera (1947) described fragmentary sauropod remains from Pampa de Agnia, Chubut, as *Amygdalodon patagonicus*. The material comes from the Cerro Carnerero Formation, which is most probably of Toarcian-Aalenian age, and thus represents the oldest Middle Jurassic archosaur-bearing unit in South America.

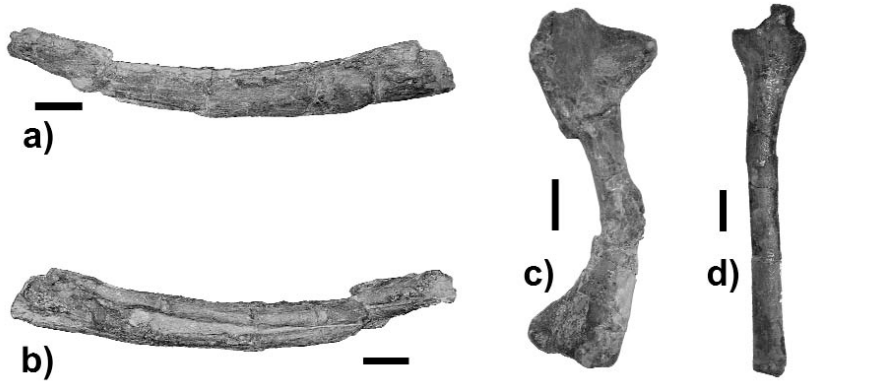

Figure 6: Pterosaur material from the Middle Jurassic Cañadón Asfalto Formation, Chubut province, Argentina. a) Left mandible in lateral view. b) Left mandible in medial view. c) Right humerus in anterior view. d) Proximal end of wing phalanx 1. Scale bars: 1 cm.

Figure 7: : Isolated pedal phalanx of a probably basal cerapodan ornithischian from the Middle Jurassic Cañadón Asfalto Formation of Chubut, Argentina, MACN CH 223. a) Dorsal view. b) Lateral view. c) Ventral view. Scale bar: 1 cm.

Additional material from the same locality was referred to this taxon and even thought to represent the same individual as the type by Casamiquela (1963), but Rauhut (2003b) showed that more than one individual is represented by these remains. Nevertheless, *Amygdalodon* still represents the oldest sauropod record from South America. The recent find of a partial sauropod sacrum from the Upper Aalenian Remoredo Formation of Neuquén, Argentina (Salgado and Gasparini 2004), demonstrates that these animals were already widely distributed in South America at the beginning of the Middle Jurassic.

Only isolated finds of fragmentary dinosaur material have been reported from the Middle Jurassic of India so far (see overview in Moser *et al.* 2006). Most of the material reported, which comes from different units in north-western India and ranges in age from the Aalenian-Bajocian to the Callovian, seems to represent sauropod dinosaurs, but only a few fragmentary remains from Khadir Island have been described in detail so far (Moser *et al.* 2006). Mainly on the basis of the morphology of a proximal fibula, Moser *et al.* (2006) concluded that some of this material represents a camarasauromorph sauropod, which would represent the oldest record of a neosauropod from the Southern Hemisphere. However, better material is needed to substantiate this claim, especially since the shape of the proximal articular surface of the element in question is rather reminiscent of sauropod metacarpals II-IV (see e.g. Ostrom and McIntosh 1966: pl. 56-58, 60-61), as is its size in comparison to other metacarpal fragments found at the same locality (Moser *et al.* 2006: figs. 4.1, 4.2).

Late Jurassic

Although the Late Jurassic is often seen as a well-known stage in the history of terrestrial vertebrates, mainly due to numerous localities in the Northern Hemisphere, such as the famous Morrison Formation of the western USA, very little is still known about Late Jurassic terrestrial vertebrates from Gondwana, and only few localities yielding archosaur material are known.

Late Jurassic archosaurs from South America were mainly known from marine crocodiles until recently. With the exception of one vertebra from Chile, reported by Gasparini (1985), all marine crocodile remains from the Late Jurassic of South America come from the Neuquén Basin in Argentina, from the Tithonian Vaca Muerta Formation and equivalent beds [Fig. 4C(1), Gasparini 1985, 1992, 1996, Gasparini and Fernandez 1997, Gasparini *et al.* 2006]. Taxa reported from these units include the metriorhynchids *Geosaurus araucanensis*, *Metriorhynchus* potens, and *Dakosaurus* andiniensis.

Pterosaurs are still very poorly known from the Late Jurassic of South America. Casamiquela (1975) reported a partial skeleton of a supposed theropod dinosaur, *Herbstosaurus pigmaeus*, found in an isolated boulder, which was later reinterpreted as a pterosaur, demonstrably from Upper Jurassic (Tithonian) strata of the Vaca Muerta Formation in Neuquén province, Argentina (Bonaparte 1981, Codorniú and Gasparini 2007). Further, mainly fragmentary fossils have been described since, including Tithonian pterosaur remains from the same beds in Argentina (Gasparini *et al.* 1987, Codorniú *et al.* 2006) and from coastal sediments of Chile (Martill *et al.* 2000), although the latter might be Early Cretaceous in age.

Dinosaurs were almost unknown from the Late Jurassic of South America until recently, with the exception of a single sauropod vertebra from unspecified Late Jurassic sediments of northern Colombia (Langston and Durham 1955) and undescribed dinosaur remains from the Late Jurassic of Chile, reported by Chong Díaz and Gasparini (1976). More recently, an isolated sauropod knee joint was reported from the Kimmeridgian Tordillo Formation of Neuquén, Argentina (García *et al.* 2003), and theropod teeth have been found in the Tacurembó Formation in Uruguay (Perea *et al.* 2003), which is probably also Late Jurassic in age (Soto, pers. comm. 2007). Salgado *et al.* (2008) described some theropod remains from the Tithonian Toqui Formation of southern Chile. This material, which includes at least one taxon of tetanurans, thus represents the southernmost Late Jurassic dinosaur body fossils known.

The most important, but still rather poorly studied Late Jurassic dinosaur fauna reported from South America so far is that of the Cañadón Calcáreo Formation of Chubut province, Argentina [Figs. 4c (2), 5]. The age of this unit is still somewhat uncertain: whereas a radiometric date puts its basal part in the Tithonian (see Rauhut 2006a), new palynological evidence seems to indicate a lowermost Cretaceous age for at least parts of the formation (Silva Nieto *et al.* 2007). More geological and stratigraphic work is needed to tie down the stratigraphic position of the dinosaurs from this formation. The first dinosaur described from the Cañadón Calcáreo Formation was *Tehuelchesaurus*, though originally thought to be

from the Middle Jurassic Cañadón Asfalto Formation (Rich *et al.* 1999). This taxon was first considered to be closely related to the Middle Jurassic Chinese sauropod *Omeisaurus* (Rich *et al.* 1999, Upchurch *et al.* 2004), but new data indicates that it is a member of the Macronaria and close to or within the Titanosauriformes (Rauhut 2002, Rauhut *et al.* 2005, Carballido *et al.* 2007). More recently, the dicraeosaurid *Brachytrachelopan mesai* (Fig. 8) and an unidentified brachiosaurid were reported from the same formation (Rauhut *et al.* 2005, Rauhut 2006a).

The most important Late Jurassic terrestrial vertebrate fauna from Gondwana known so far comes undoubtedly from the famous Tendaguru Beds of Tanzania [Fig. 4C(3), Maier 2003]. Archosaurs from three different levels within the Tendaguru Beds include crocodile teeth, isolated pterosaur remains, and numerous taxa of dinosaurs (Janensch 1914, Russell *et al.* 1980, Aberhan *et al.* 2002, Maier 2003). The ages of the three different beds are probably Oxfordian for the Lower Saurian Bed, Kimmeridgian-Early Tithonian for the Middle Saurian Bed, and Late Tithonian to earliest Cretaceous for the Upper Saurian Beds (Aberhan *et al.* 2002).

Crocodiles are so far only represented by isolated teeth from the Upper Saurian Beds, which seem to be similar to those of the Early Cretaceous neosuchian *Bernissartia* (Maier 2003: 315). *Pterosaurs* are represented by numerous, but mainly isolated and often fragmentary elements. Most pterosaur remains come from the Upper Saurian Beds, though they are also present in the Middle Saurian Beds (Reck 1931). Reck (1931) described four species on the basis of this material, though mainly based on uncomparable remains: *Rhamphorhynchus tendagurensis, Pterodactylus maximus, Pterodactylus brancai*, and *Pterodactylus arningi*, all from the Upper Saurian Beds. However, the validity of all of these species is highly questionable (Unwin and Heinrich 1999). Galton (1980a) referred another specimen, probably from the Middle Saurian Bed, to *P. brancai* and transferred this species to the Early Creatceous Asian genus *Dsungaripterus*. Interestingly, Unwin and Heinrich (1999) described a pterosaurian jaw fragment from the Middle Saurian Beds as a new species, *Tendaguripterus recki*, which they also referred to the Dsungaripteroidea. However, since the type and referred specimens of *"Dsungaripterus" brancai* are tibiotarsi, more material is necessary to establish whether only one, or two taxa of dsungaripteroids were present in the Tendaguru fauna.

The dinosaur fauna from Tendaguru is dominated by sauropods, which are represented by at least seven species, the brachiosaurid *Brachiosaurus brancai*, the probably basal titanosaurs *Janenschia robusta* and *Tendaguria tanzaniensis* (which might be conspecific), the dicraeosaurids *Dicraeosaurus hansemanni* and *D. sattleri*, and the diplodocids *Tornieria africana* and *Australodocus bohetii* (Janensch 1914, 1929, Bonaparte *et al.* 2000, Upchurch *et al.* 2004, Remes 2006, 2007). Theropod dinosaurs are represented by the basal neoceratosaur *Elaphrosaurus bambergi* (Fig. 9) and at least six more taxa (Janensch 1920, 1925, Rauhut 2005b, c, 2006b). The theropod fauna seems to be dominated by basal tetanurans and neoceratosaurs, whereas coelurosaur remains could not be identified so far (Rauhut 2005b, c, 2006b). Ornithischians are much less diverse and are represented only by the stegosaur *Kentrosaurus aethiopicus* and the small ornithopod *Dysalotosaurus lettowvorbecki* (Hennig 1925, Janensch 1955). Dinosaur remains are not evenly distributed in all levels at Tendaguru. The Lower Saurian Beds have only yielded a few theropod teeth attributed to "*Megalosaurus*" *ingens* (Janensch 1925) and fragmentary sauropod remains, possibly representing *Brachiosaurus* (Aberhan *et al.* 2002). The Middle and Upper Saurian Beds are much richer in vertebrate remains, but differ slightly in their dinosaur fauna. The Middle Saurian Beds contain remains of the sauropods *Brachiosaurus brancai, Dicraeosaurus hansemanni, Tornieria africana*, and *Australodocus bohetii* (Aberhan *et al.* 2002, Remes 2006, 2007), the theropods *Elaphrosaurus bambergi* and at least four more taxa, including two tetanurans and two ceratosaurs (Janensch 1925, Rauhut, unpublished data). Both ornithischians known from Tendaguru, *Kentrosaurus aethiopicus* and *Dysalotosaurus lettowvorbecki*, are also present in the Middle Saurian Beds (Aberhan *et al.* 2002). The Upper Saurian Beds have yielded the sauropods *Brachiosaurus brancai, Janenschia robusta*, *Tendaguria tanzaniensis*, *Dicraeosaurus sattleri*, and *Tornieria africana*, at least two ceratosaurian and two tetanuran theropods (Rauhut 2005c, unpublished data), and the stegosaur *Kentrosaurus aethiopicus* (Aberhan *et al.* 2002).

Another dinosaur fauna reported from the Upper Jurassic of Africa comes from the Kadsi Formation of Zimbabwe [Fig. 4c(4), Raath and McIntosh 1987], but the material collected so far is fragmentary and identifications of taxa have to be treated with caution. Raath and McIntosh (1987) identified at least four, possibly five sauropod taxa from these beds, and referred them to the genera *Brachiosaurus, Janenschia* (=*Tornieria* in the cited work, for the convoluted taxonomic history of this genus see Wild 1991), *Dicraeosaurus, Barosaurus*, and, possibly, *Camarasaurus*. However, only the remains referred to *Brachiosaurus* might be diagnostic on generic level, the rest of the material would better be understood as basal titanosaur indet., two diplodocoids indet. (possibly a dicraeosaurid and a diplodocid), and an unidentified sauropod. Two theropod femora, tentatively identified as ?allosaurid by Raath and McIntosh (1987: 109, 113 fig. 4) might rather represent a large neoceratosaur, as indicated by the low, aliform lesser trochanter with a well-developed trochanteric shelf.

A further Late Jurassic unit from Africa has yielded archosaur remains, the Mugher Mudstone Formation of Ethiopia, which is of probably Tithonian age (Goodwin *et al.* 1999). Archosaur fossils from this formation include a possibly goniopholid crocodile and theropod,

sauropod, and probable ornithischian teeth (Werner 1995, Goodwin *et al.* 1999). One theropod tooth fragment was identified as cf. *Acrocanthosaurus* by Goodwin *et al.* (1999: 735-736), but the only character given in support of this assignment (chisel-shaped denticles) actually represents the plesiomorphic condition in theropods, so this specimen should be regarded as Theropoda indet. From slightly older levels close to the city of Harrar in Ethiopia (Oxfordian-Kimmeridgian), Huene (1938) described a partial mandibular symphysis as a new pliosaur, *Simolestes nowackianus*, but this specimen was later assigned to the thalattosuchian crocodyliform *Machimosaurus* by Bardet and Hua (1996), thus representing the oldest record of this group in Africa.

JURASSIC ARCHOSAURS FROM THE NORTHERN HEMISPHERE

Jurassic archosaurs from the Northern Hemisphere are known from a number of localities.

In the Early Jurassic, the probably most important Laurasian localities are the Kayenta Formation and Navajo Sandstone and equivalent beds of the western USA [Fig. 4A(5)], the Newark Supergroup of eastern North America [Fig. 4a(6)], the Posidonia Shale in Germany and comparable strata in England and France [Fig. 4a(7)], and the Lufeng Formation of south-eastern China [Fig. 4a(8)].

In the Middle Jurassic, important faunas are known especially from various, mainly marine units in England and France [Fig. 4b(6)] and the Lower Shaximiao Formation of Sichuan, China [Fig. 4b (8)]. Furthermore, the Upper Shaximiao Formation of China [Fig. 4c(9)], often considered to be Late Jurassic in age (e.g. Weishampel *et al.* 2004, Peng *et al.* 2005), might also be of late Middle Jurassic (Callovian) age (Averianov *et al.* 2005, 2007). Averianov *et al.* (2005) cited the supposed close relationships of the Chinese sauropod *Omeisaurus* with the supposedly Middle Jurassic South American sauropod *Tehuelchesaurus* as evidence for a Middle Jurassic age, but, as noted above, *Tehuelchesaurus* neither comes from Middle Jurassic sediments, nor is it closely related to *Omeisaurus*. However, Averianov *et al.* (2007) further mentioned invertebrate evidence for a Middle Jurassic age the Upper Shaximiao Fm. On the other hand, the fauna of the Upper Shixamiao Formation shares the dinosaur genera *Sinraptor* and *Mamenchisaurus* with the Shishougou Formation of Xinjiang, China, which is considered to be Oxfordian in age (Xu *et al.* 2006a, Xu, pers. comm. to OR 2006), so the age of this unit is best considered to be uncertain.

The most important Late Jurassic faunas are certainly those of the Morrison Formation of the western USA [Fig. 4c(5)], various Kimmeridgian units in Portugal [Fig. 4c(6)], the Solnhofen Limestone in southern Germany [Fig. 4c(7)], and various units in China, including the Shishougou Formation of Xinjiang [Fig. 4c(8)].

Early Jurassic

In the Northern Hemisphere, crocodiles are well known from marine forms, as in the Southern Hemisphere. The oldest northern records of thalattosuchians are contemporaneous to those in the Southern Hemisphere and were found in the Sinemurian of France (see Gasparini *et al.* 2000, Mueller-Töwe 2006). Thalattosuchians are especially well-represented in the Toarcian of the Posidonia Shale and contemporaneous sediments in Europe, from where the genera *Pelagosaurus, Platysuchus* and *Steneosaurus* are known, the latter with several species (Mueller-Töwe 2006). In this stage, fragmentary thalattosuchian remains are also known from North America and China (Mueller-Töwe 2006).

Terrestrial Early Jurassic crocodiles are known from the western US, from where several taxa of "sphenosuchians" (the monophyly of which is still controversial, see Clark and Sues 2002 and Sues *et al.* 2003) and protosuchids and the oldest known goniopholid, *Calsoyasuchus*, were reported (Colbert and Mook 1951, Crompton and Smith 1980, Sues *et al.* 1994, Clark and Sues 2002, Tykoski *et al.* 2002). A similar faunal composition, with protosuchids and "sphenosuchians" is also found in the McCoy Brook Formation of the Newark Supergroup of eastern North America (Shubin *et al.* 1994, Sues *et al.* 1996) and the Lufeng Formation of China (Simmons 1965, Luo and Wu 1994, Wu and Sues 1996, Harris *et al.* 2000).

Pterosaurs are known from a number of Early Jurassic Laurasian localities, though most remains are fragmentary, such as the type of *Rhamphinion* from the Kayenta Formation of the western USA (Padian 1984, Sues *et al.* 1994). However, such specimens might provide important anatomical information as well (*e.g.* Clark *et al.* 1998). Well-preserved pterosaur remains have been found in the Posidonia Shale of Germany (see Padian and Wild 1992) and the Lias of Lyme Regis in England (see Padian 1983). These remains represent the families Dimorphodontidae and Campylognathidae.

Dinosaurs are also known from a variety of Early Jurassic localities in the Northern Hemisphere. Taxa recorded include basal thyreophoran ornithischians from western North America (Colbert 1981, Padian 1989), Europe (Owen 1863, Haubold 1990) and Asia (Simmons 1965, Dong 2001, Norman *et al.* 2007). Theropods are represented by coelophysoids in North and Central America (Tykoski and Rowe 2004, Munter and Clark 2005, Tykoski 2005), Europe (Carrano and Sampson 2004) and Asia (Irmis 2004) and "dilophosaurs" in North America (Welles 1954, 1984) and Asia (Hu 1993, see also Smith *et al.* 2007). A therizinosauroid theropod reported from the Lufeng Formation (Xu *et al.* 2001) is of doubtful affinities, and might represent a prosauropod (Rauhut 2003c). Basal sauropodomorphs ("prosauropods") are well-documented from the Lufeng Formation of China (Young 1941, 1951,

Zhang and Yang 1995), but they are also present in both western and eastern North America (Attridge *et al.* 1985, Galton 1976, Yates 2004). Furthermore, Early Jurassic sauropods are known from China (*e.g.* He *et al.* 1998, Barrett 1999, Upchurch *et al.* 2007) and Europe (Wild 1978).

Middle Jurassic

As for the Southern Hemisphere, the Middle Jurassic archosaur record from the Northern Hemisphere is rather poor, and, most notably, only one skeletal remain of an archosaur from that period, the poorly preserved type specimen of the crocodyliform *Entradasuchus*, has been described from North America (Hunt and Lockley 1995), though dinosaurs are known from track evidence (e.g. Kvale *et al.* 2001). Middle Jurassic crocodiles from Europe are represented by isolated teeth attributed to atoposaurids and goniopholids in England (Evans and Milner 1994) and France (Kriwet *et al.* 1997) and marine thalattosuchians from various countries (Mueller-Töwe 2006). The record of these marine crocodyliforms is poor in the Aalenian and Bajocian, although the first metriorhynchids are known from the latter stage (Mueller-Töwe 2006). In the Bathonian and Callovian, both teleosaurid and metriorhynchid thallatosuchians are well-represented especially in England and France, although some remains are also known from central Asia (Mueller-Töwe 2006). Middle Jurassic terrestrial crocodiles from Asia include a goniopholid and the enigmatic *Hsisosuchus* from the Lower Shixaniao Formation (Peng *et al.* 2005), as well as a "sphenosuchian" from the Wuceiwan Formation (Clark *et al.* 2004) and a goniopholid from the Totunhe Formation in China (Maisch *et al.* 2003), and a report of a goniopholid from Kirghizia (Averianov 2000).

The most important Middle Jurassic dinosaur fauna from the Northern Hemisphere is that of the (?) Bathonian Lower Shaximiao Formation of China (Peng *et al.* 2005), which includes stegosaurian (Maidment and Wei 2006) and basal cerapodan ornithischians (Barrett *et al.* 2005), theropods, and sauropods. Theropods include basal tetanurans, such as *Xuanhanosaurus* and *"Szechuanosaurus" zigongensis* (Dong 1984, Gao 1993), and the possible basal coelurosaur *Gasosaurus* (Dong and Tang 1985, Holtz *et al.* 2004). The sauropod fauna is dominated by mamenchisaurids (Peng *et al.* 2005), but also includes the basal sauropod *Shunosaurus* and the possibly oldest known neosauropods (Upchurch *et al.* 2004). Another close relative of neosauropods or a basal member of this clade is also known from the Callovian Balabansai Formation of Kirghizia [Fig. 4b(7), Alifanov and Averianov 2003]. Ornithischians are represented in the same formation by an indeterminate stegosaur (Averianov *et al.* 2007) and isolated teeth that were described as the oldest known pachycephalosaur (Averianov *et al.* 2005). However, the teeth are rather poorly preserved and the identification is questionable.

Although some of the first dinosaurs to be described were Middle Jurassic taxa from Europe (*e.g.* Buckland 1824), Middle Jurassic dinosaurs from this continent are still poorly understood, mainly due to the fragmentary nature of most remains. However, the fauna includes non-neosauropodan sauropods (Upchurch and Martin 2002, 2003), the basal spinosauroids *Eustroptospondylus* (Walker 1964, Holtz *et al.* 2004), *Dubreuillosaurus* (Allain 2002, 2005) and *Poekilopleuron* (Allain and Chure 2002), and one of the oldest coelurosaurs, *Proceratosaurus* (Woodward 1910, Holtz 2000, Rauhut 2003c). Ornithischian dinosaurs are represented by stegosaurs (Galton and Powell 1983, Galton 1990), ankylosaurs (Galton 1983) and basal ornithopods (Galton 1980b, Evans and Milner 1994, Kriwet *et al.* 1997, Ruiz-Omeñaca *et al.* 2005).

Late Jurassic

One of the most important Late Jurassic archosaur faunas is certainly that of the Morrison Formation of western North America (see Foster 2003). Crocodiles from this unit include some of the last "sphenosuchians" known (Walker 1970, Göhlich *et al.* 2005), a cursorial basal mesoeucrocoylian and other cursorial crocodylomorphs of unspecified systematic position, the probable atoposaurid *Hoplosuchus,* several species of *Goniopholis*, and the goniopholid *Eutretauranosuchus* (Tykoski *et al.* 2002, Foster 2003, Pol and Gasparini 2007: fig. 5.5). Pterosaurs are poorly represented in the terrestrial deposits of the Morrison Formation, but include at least one "rhamphorhynchoid" and several taxa of pterodactyloids (Foster 2003). The dinosaur fauna of the Morrison Formation is the most diverse fauna known from the Jurassic, and one of the most diverse Mesozoic dinosaur faunas known in general (see Weishampel *et al.* 2004). The dinosaur fauna includes several species of diplodocid sauropods, the basal macronarian *Camarasaurus* as the most abundant taxon among the sauropods, the basal titanosauriform *Brachiosaurus altithorax*, *Haplocanthosaurus*, which either represents a basal diplodocoid, or a basal macronarian, and the probably basal diplodocoid *Amphicoelias* (Wilson 2002, Foster 2003, Upchurch *et al.* 2004). The theropod fauna includes rare ceratosaurs (Marsh 1884, Galton 1982, Madsen and Welles 2000, Chure 2001) and basal spinosauroids (Britt 1991, Holtz *et al.* 2004), abundant allosaurids (Madsen 1976, Foster 2003), and a variety of coelurosaurs (Foster 2003, Holtz *et al.* 2004, Carpenter *et al.* 2005). Ornithischians are represented by rare heterodontosaurids (Galton 2005), several stegosaurian and ankylosaurian thyreophorans (Kirkland and Carpenter 1994, Carpenter *et al.* 1998, 2001, Galton and Upchurch 2004) and diverse ornithopods (Foster 2003, Norman *et al.* 2004, Norman 2004, Galton 2005).

Another northern fauna of particular interest in biogeographic terms is that from central America and the Caribbean (see *e.g.* Gasparini and Iturralde-Vinent 2006). Taxa reported from that area in-

clude metriorhynchid crocodiles (Gasparini and Iturralde-Vinent 2001, Buchy *et al.* 2006, 2007) and rhamphorhynchid pterosaurs (Colbert 1969, Gasparini *et al.* 2004).

In Europe, several units of Kimmeridgian age in Portugal have yielded a fauna that is closely comparable to that of the Morrison Formation. Furthermore, the Kimmeridgian-Tithonian lithographic limestones of southern Germany have yielded a rich fauna of mainly non-dinosaurian archosaurs, marine crocodiles are known from a number of Late Jurassic formations, and several isolated archosaur remains have been reported from various localities.

European Late Jurassic crocodiles include goniopholids (e.g. Schwarz 2002), atoposaurids (*e.g.* Wellnhofer 1971), teleosaurid and metriorhynchid thalattosuchians (see Mueller-Töwe 2006), and some mesoeucrocodylian taxa of uncertain affinities, such as the enigmatic *Lisboasaurus* and *Lusitanosuchus* (Buscalioni *et al.* 1996, Krebs and Schwarz 2000, Schwarz and Fechner 2004). Pterosaurs are especially represented by the rich faunas of the Solnhofen limestone (see especially Wellnhofer 1970, 1975), but are also known from fragmentary material from other localities (*e.g.* Wiechmann and Gloy 2000, Fastnacht 2005). Taxa reported in-clude the enigmatic "frog-mouthed" anuroganthids (Wellnhofer 1975, Bennett 2007), scaphognathine and rhamphor-hynchine rhamphorhynchids (Wellnhofer 1975), ctenochasmatoids (Wellnhofer 1970, Unwin 2003, Jouve 2004), and dsungariptoroids (Wellnhofer 1970, Un-win 2003, Fastnacht 2005).

Late Jurassic dinosaurs from Europe include ceratosaurian, basal spinosauroid, allosauroid, and various coelurosaurian theropods, brachiosaurid and diplodocid sauropods, and stegosaurian and ornithopodan ornithischians from Portugal (Antunes and Mateus 2003, Mateus 2006, Mateus *et al.* 2006), basal coelurosaurs and the basal bird *Archaeopteryx* from the lithographic limestones of southern Germany (Ostrom 1978, Wellnhofer 1992, Mayr *et al.* 2005, Göhlich and Chiappe 2006), and some other finds of similar taxa from various localities (see Weishampel *et al.* 2004).

In China, Late Jurassic archosaurs are mainly known from the Upper Shaximiao Formation (though see comments on the age of this formation above) and the Shishougou Formation. Crocodiles reported include basal crocodyliforms (Peng *et al.* 2005) and goniopholids (see Wu *et al.* 1996), as well as another species of *Hsisosuchus* (Peng *et al.* 2005). Late Jurassic pterosaurs from Asia are rare, but include at least the ctenochasmatid *Huanhepterus* (Dong 1982).

Dinosaurs from the Late Jurassic of Asia include sinraptorid allosauroids, mamenchisaurid sauropods, and stegosaurian and ornithopodan ornithischians (Weishampel *et al.* 2004, Peng *et al.* 2005, Maidment and Wei 2006). Furthermore, the oldest ceratopsian ornithischians are known from the Tithonian Tuchengzi and the Oxfordian Shishougou formations of China (Zhao *et al.* 1999, Xu *et al.* 2006b), and the latter unit has also yielded the basal tyrannosauroid *Guanlong* (Xu *et al.* 2006a) and the first ceratosaurs from Asia (Xu and Clark 2006).

JURASSIC ARCHOSAUR EVOLUTION: A SOUTHERN PERSPECTIVE

Quality of the Jurassic archosaur fossil record

From the above, it is clear that the Jurassic archosaur fossil record is far from complete, both stratigraphically and geographically (Figs. 4, 10), and our understanding of Jurassic archosaur evolution is actually based on surprisingly few localities (Fig. 4). Whereas several important faunas are known in the Early Jurassic (Upper Elliot and Clarens Formations in Africa, Navajo Sandstone, Kayenta Formation and equivalent beds in North America, Posidonia Shale and equivalent beds in Europe, Lufeng Formation in Asia) and the Late Jurassic (Tendaguru Beds in Africa, Morrison Formation in North America, various units in Portugal and Solnhofen limestones in Europe, Shishougou Formation in Asia), Middle Jurassic archosaurs are almost entirely known from isolated finds, often also fragmentary. This is especially true for the early Middle Jurassic (Aalenian-Bajocian), whereas at least one important fauna is known from the Bathonian-Callovian, that of the Lower Shaximiao Formation of China (Peng *et al.* 2005). This underscores the potential importance of the Late Middle Jurassic Cañadón Asfalto Formation of Chubut, Argentina. Although mainly dinosaurs and mammals have been described from this formation so far (Bonaparte 1979, 1986, Rauhut *et al.* 2002, Rauhut 2003a, 2005a, Rougier *et al.* 2007a, b), abundant remains of other vertebrates have also been found, but not described in detail yet, including well-preserved pterosaurs (Unwin *et al.* 2004) and remains of crocodiles (Rauhut *et al.* 2001), potentially making this unit a southern counterpart of the Lower Shaximiao Formation.

However, on stage level, biases in stratigraphic distribution are also found in other epochs of the Jurassic. Thus, Oxfordian archosaurs are still very poorly known, with the Shishougou Formation of China basically representing the only productive formation of that age. Likewise, several stages of the Early Jurassic might be underrepresented, though interpretation is hampered here by the uncertain dating of almost all known terrestrial vertebrate localities of this epoch.

Concerning the geographic distribution of Jurassic archosaurs, their fossil record is strongly biased towards faunas from the Northern Hemisphere, which becomes evident when looking at the dinosaur record from the Jurassic (Fig. 11). For the entire Jurassic, 121 valid species of dinosaurs are recognized from Laurasian continents, whereas only 27 have been described from Gondwana (as of October 2007, only formally named taxa have been considered, OR & ALA, unpublished data). For the different

epochs of the Jurassic, the numbers are more even for the Early Jurassic (19 species in Laurasia, 10 species in Gondwana), but very strongly biased towards northern faunas in the Middle (34 to 8) and especially the Late Jurassic (68 to 9). Thus, most scenarios of Jurassic archosaur evolution are largely or even entirely based on the fossil record of the Northern Hemisphere. This makes interpretation of evolutionary events often very difficult, and especially the hypothesis of increased endemism in terrestrial archosaurs in response to the initial breakup of Pangea is hard to test in the absence of suitable localities in the Southern Hemisphere. For example, until recently it was difficult to evaluate the observed differences between the Laurasian Late Jurassic dinosaur fauna and that from the Tendaguru Beds in Tanzania, since, in the absence of other Late Jurassic dinosaur faunas from Gondwana, it was impossible to decide whether these differences reflect differential evolution of the faunas, or maybe just different ecological settings of the localities. Indeed, given this paucity in comparative faunas, more emphasis has been laid on the supposed similarities of the Tendaguru fauna and those of the Morrison Formation and Late Jurassic Portuguese localities, and a variety of biogeographical hypotheses have been proposed to explain these similarities (*e.g.* Lull 1915, Galton 1977, 1982, Mateus 2006). Fortunately, the newly recognized fauna from the Cañadón Calcáreo Formation of Argentina (Rich *et al.* 1999, Rauhut et al. 2005, Rauhut 2006a, c) might help to put the Tendaguru fauna in a Gondwanan context, once more material is excavated and studied (see also below).

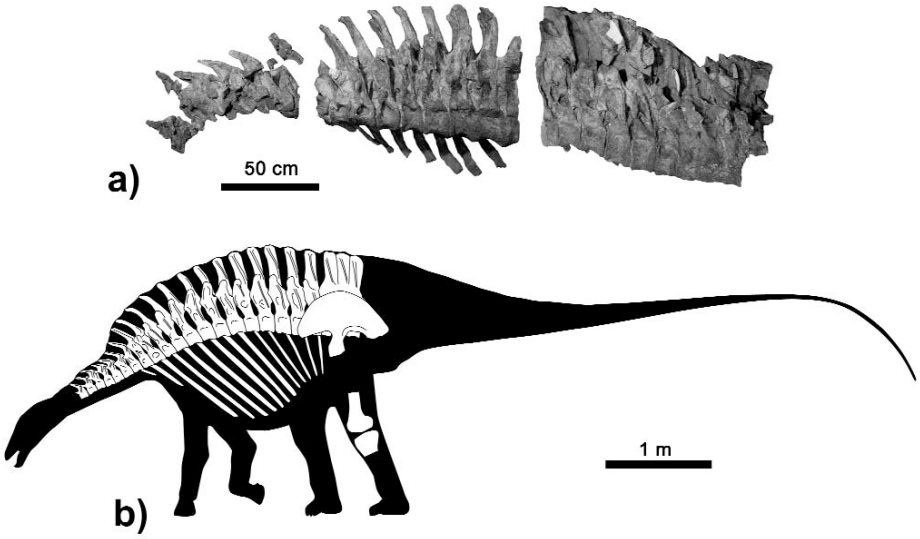

Figure 8: *Brachytrachelopan mesai* from the (?)Tithonian Cañadón Calcáreo Formation, Chubut province, Argentina. a) Vertebral column as preserved (MPEF PV 1716). b) Outline reconstruction showing preserved elements.

Taking both the stratigraphic and geographic bias in Jurassic archosaur distribution into consideration, especially the Gondwanan archosaur record of this time can only be called patchy (Figs. 4, 10). In terms of marine crocodiles, South America certainly has the most complete record of all Gondwanan continents, with thalattosuchians known from most stages from the Sinemurian to the Tithonian. Concerning terrestrial Jurassic archosaur faunas, Africa has the most complete record, with remains known from almost the entire Early Jurassic, the latter stages of the Middle Jurassic, and the upper stages of the Late Jurassic, though a lot of especially the Middle Jurassic finds are isolated occurrences. In South America, only the later Middle Jurassic is well represented by the fauna from the Cañadón Asfalto Formation, though with great potential for new discoveries in both the Early and the Late Jurassic in Argentina. All other Gondwanan continents have only isolated occurrences, in the Early Jurassic in India and Antarctica, and in the Middle Jurassic in Australia. However, it must be noted that

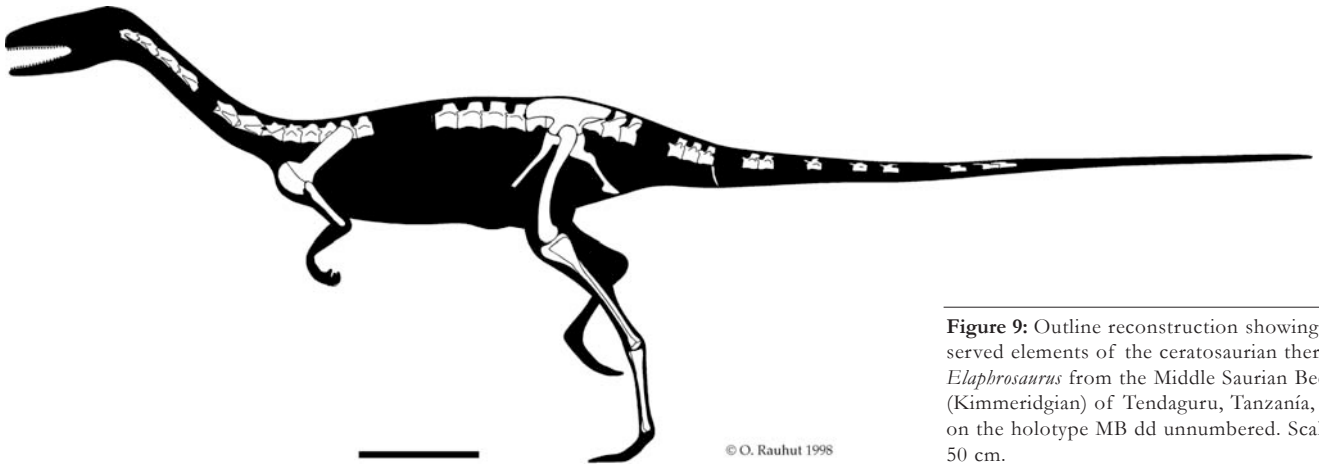

Figure 9: Outline reconstruction showing preserved elements of the ceratosaurian theropod *Elaphrosaurus* from the Middle Saurian Beds (Kimmeridgian) of Tendaguru, Tanzanía, based on the holotype MB dd unnumbered. Scale bar: 50 cm.

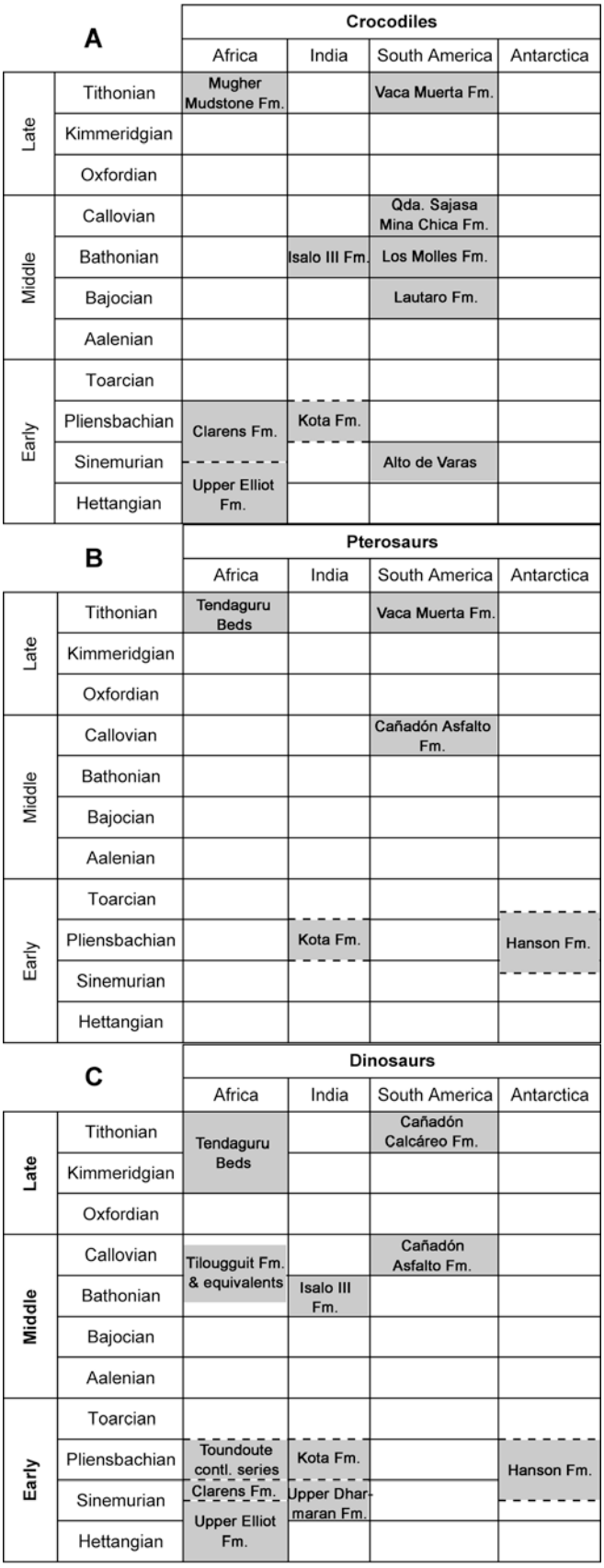

Figure 10: Stratigraphic completeness of the archosaur fossil record of Gondwana. a) Crocodiles. b) Pterosaurs. c) Dinosaurs. Dotted lines indicate uncertain limits of the stratigraphic range of a certain geological unit. Some minor localities with fragmentary and uninformative material have been omitted, in the chart for dinosaurs, only localities that have yielded at least two identifiable taxa are shown. India includes Madagascar, since these two areas were geographically united in the Jurassic.

even for the Jurassic stages with faunas known in the Gondwanan continents, these are usually single localities or formations, and comparable material from other parts of the continent is usually absent.

Faunal composition, evolutionary considerations and biogeography

a) Marine crocodiles: The evolutionary and biogeographic significance of the thalattosuchian crocodiles, especially of South America, has been discussed at length by Zulma Gasparini and co-workers (*e.g.* Gasparini 1985, 1992, 1996, Gasparini and Fernandez 1997, Gasparini *et al.* 2000, 2005, 2006), so only the most important aspects will be outlined here.

The occurrence of thalattosuchian crocodiles in the Sinemurian of Chile (Chong Diaz and Gasparini 1972) and western Argentina (Huene 1927), and, probably, the Early Jurassic of India (Bandyopadhyay *et al.* 2002) demonstrates that this clade did not only have a circumtethyan distribution in the Early Jurassic, but also already entered the Pacific region. This dispersal most probably happened through the Hispanic corridor (Gasparini *et al.* 2000), which was sporadically open since at least the Pliensbachian (Aberhan 2001), though the contemporaneous occurrence of the first thalattosuchians in the Sinemurian of Europe and Chile might indicate that marine faunal exchanges may have been possible even before.

With the repeated opening and closing of the Hispanic corridor during the Middle Jurassic (Westermann 1993, Moyne *et al.* 2004), there might have been an exchange of marine crocodiles between the Pacific and the Tethys every time the corridor was in effect. This exchange was probably not unidirectional; whereas the oldest representative of *Metriorhynchus* is found in Chile (Gasparini *et al.* 2000), and the genus only later appears in Europe (Mueller-Töwe 2006), *Geosaurus* is first known in Europe, and only subsequently in South America (Pol and Gasparini

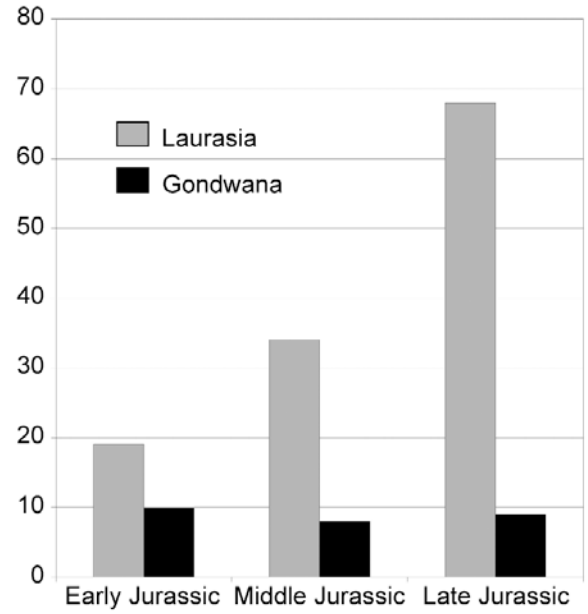

Figure 11: Valid dinosaur species from the Jurassic of the Northern and Southern Hemisphere (as of October 2007, OR & ALA unpublished data).

2007). The evolution of thalattosuchians in the Middle Jurassic might thus be characterized by periods of dispersal separated by periods of cladogeneses in separation in the Tethys and the Pacific. Thus, the Hispanic corridor might have been a "motor" of thalattosuchian evolution in the Middle Jurassic, though this hypothesis needs further testing by new finds and rigorous cladistic and biogeographic analyses of all species of Middle and Late Jurassic thalattosuchians.

The exchange between the Tethyan region and the Pacific continued during the Late Jurassic, when the Hispanic corridor was permanently open (Ford and Golonka 2003), as evidenced by shared genera of metriorhynchids, such as *Geosaurus* and *Dakosaurus*. It is interesting, though, that, whereas all three genera of metriorhynchids (*Metriorhynchus*, *Geosaurus* and *Dakosaurus*) are present in both areas, no teleosaurids have been reported from the Late Jurassic of western South America so far, although they are present both in the northern and southern part of the Tethys during this period (*e.g.* Krebs 1967, Bardet and Hua 1996). This might be due to the more fully marine environments represented by the thalattosuchian-bearing sediments in Chile and Argentina (Gasparini *et al.* 1999), and further finds of marine reptiles from nearshore environments will have to show whether this group was truly absent from the Pacific coast of South America.

b) Terrestrial crocodiles: Interpretation of the evolution of terrestrial crocodiles in Gondwana during the Jurassic is hampered by the abysmal fossil record of these animals in the Middle and Late Jurassic of the Southern Hemisphere. In the Early Jurassic, the first successful radiations of the crocodylomorph lineage, the "sphenosuchians" and basal crocodyliforms ("protosuchians"), had a Pangean distribution, as evidenced by the occurrence of these groups in southern Africa, North America and China during this time. Phylogenetic relationships among crocodylomorphs, especially the presence of the advanced mesoeucrocodylian lineages Thalattosuchia and Goniopholidae in the Early Jurassic, indicate that the major radiation of mesoeucrocodylians already happened during this period (Pol and Gasparini 2007), but most lineages are poorly represented globally before the Late Jurassic. The presence of possible atoposaurids in the Middle Jurassic in Madagascar and a possible goniopholid in the Late Jurassic of Tanzania, if the identity of these fragmentary remains can be confirmed, might show that these more advanced mesoeucrocodylians were also globally distributed before the final separation of the continents of the Northern and Southern Hemisphere. Furthermore, the atoposaurid record from Madagascar (Flynn *et al.* 2006) is roughly contemporaneous with the oldest records of this group in the Northern Hemisphere (*e.g.* Kriwet *et al.* 1997), indicating that derived members of this lineage might originated already considerably earlier.

However, the lack of two important mesoeucrocodylian lineages, which are especially widely distributed in the Southern Hemisphere during the Cretaceous, the notosuchians and the peirosaurids (Fig. 1, see Pol and Gasparini 2007), during the Jurassic is striking. Two possible scenarios might explain the lack of these clades in the fossil record during the Jurassic. First, both groups might have been genuinely rare during the Jurassic and were maybe restricted to a small region, and only experienced their great radiation in the Cretaceous. Alternatively, both groups might have been largely restricted to the Southern Hemisphere already in the Jurassic, but not necessarily been rare, and have not been reported so far due to the extremely poor record of terrestrial vertebrates in the Jurassic of Gondwana. Which of these scenarios, which might not be completely exclusive, is correct can only be demonstrated by more material of terrestrial crocodiles from the Southern Hemisphere.

c) Pterosaurs: As in the case of the terrestrial crocodiles, the extremely poor Jurassic Gondwanan record of pterosaurs severely restricts any interpretation of their evolutionary history in the Southern Hemisphere. From the scarce remains, it is evident that pterosaurs were already present in Gondwana in the Early Jurassic. However, pterosaur remains are unknown from the best known Early Jurassic vertebrate fauna from the Southern Hemisphere, that of the Upper Stormberg Group of South Africa, despite the fact that the Upper Elliot Formation frequently preserves small vertebrate remains in often exquisite detail. This might indicate that these animals

might have been very rare in southern Gondwana at that time. That pterosaurs had colonized even southern Gondwana by the Early Jurassic is shown by the isolated humerus found in the Hanson Formation of Antarctica (Smith and Pol 2007).

If confirmed, the occurrence of a pterodactyloid in the Callovian Cañadón Asfalto Formation of Argentina would be the earliest record of this clade globally, which, in the Northern Hemisphere appears abruptly in the fossil record with many different clades in the Kimmeridgian-Tithonian (Unwin 2006). Once properly studied, the pterosaur fauna from the Cañadón Asfalto Formation might prove to be of great importance for our understanding of pterosaur evolution, since it represents one of the very few strictly terrestrial faunas that have yielded abundant and well-preserved pterosaur material (see Buffetaut 1995).

From the Late Jurassic, only pterodactyloid pterosaurs have been reported from South America so far (Martill *et al.* 2000, Codorniú and Gasparini 2007), but both "rhamphorhynchoids" and pterodactyloids are present in eastern Africa (Reck 1931, Galton 1980, Unwin and Heinrich 1999). Again, the wide distribution of pterydactyloids indicates that their evolution and radiation was well under way by the time the first members of this clade appear in the fossil record. Furthermore, the occurrence of dsungaripteroids in Europe (see Unwin 2003, Fastnacht 2005), Africa (Unwin and Heinrich 1999) and, possibly, South America (Martill *et al.* 2000) indicates a still global distribution of these animals in the Late Jurassic, as might be expected from clade of actively flying animals, and is also still found in the Cretaceous for several pterosaur clades, despite the separation of continental masses (Unwin 2006).

Again, more fossil finds from Gondwanan localities are needed to better understand pterosaur evolution during the Jurassic.

d) Dinosaurs: Compared to the other groups discussed above, dinosaurs certainly have the best Jurassic fossil record in the Southern Hemisphere, though their record is certainly far from complete, and even very poor if compared with that of the Northern Hemisphere (see above). Thus, all interpretations of Jurassic dinosaur evolution in Gondwana should be regarded as tentative, and might easily change in the light of new discoveries.

Early Jurassic dinosaurs faunas, especially that of the Elliot and Clarens formations and equivalent beds in Zimbabwe in southern Africa highlight the close faunal relationships in different parts of Pangea at that time. Basal thyreophoran ornithischians are present in basically all important Early Jurassic dinosaur localities, in southern Africa (Butler *et al.* 2008), the Kota Formation of India (Nath *et al.* 2002, see above), the Kayenta Formation of western North America (Colbert 1981, Padian 1989), the Liassic of Europe (Owen 1863, Haubold 1990), and the Lufeng Formation of China (Norman *et al.* 2007). This global distribution gives testimony to the rapid evolution of thy-reophorans, which seem to represent one of the first successful radiations of ornithischians, soon after the origin of this group in the Late Triassic.

Another group of ornithischians from southern Africa is of special interest as well, the heterodontosaurids. Heterodontosaurids represent the most diverse and abundant group of ornithischians in the Upper Elliot and Clarens Formations (Butler 2005, Knoll 2005), but they seem to be rare in the Northern Hemisphere, from where only one undescribed heterodontosaurid from the Kayenta Formation has been reported (Sereno pers. com. in Butler 2005). The fact that heterodontosaurids probably represent the most basal clade and thus the earliest radiation of ornithischian dinosaurs (Butler *et al.* 2008), together with the occurrence of the basalmost ornithischians known in the Late Triassic of South America (Casamiquela 1967, Ferigolo and Langer 2007), including the oldest known heterodontosaurid (Báez and Marsicano 2001), and southern Africa (Butler *et al.* 2007), indicates that the origin and early diversification of ornithischians is probably found in southern Gondwana. The phylogenetic position of *Lesothosaurus* as the basalmost thyreophoran known and of *Stormbergia* as the basalmost cerapodan (Butler *et al.* 2008) is in general accordance with this interpretation (Fig. 12).

Thus, the poor Gondwanan fossil record in the Middle Jurassic might account for our still rather poor understanding of the early Mesozoic radiation of ornithischians, since the major radiation of this group, in which basically all important lineages were established, took place during this time (Sereno 1999a, Butler *et al.* 2008). It is interesting, however, to note that ornithischians seem to have been rather rare in the Middle Jurassic of Gondwana, where they have only been reported in the best known fauna, that of the Cañadón Asfalto Formation (see above), and here they seem to be amongst the rarest vertebrate groups represented in general (OR, pers. obs.). Nevertheless, the wide distribution and diversity of ornithischians on higher taxonomic level in the Late Jurassic indicates that much of this radiation took place during Pangean times in the Early or Middle Jurassic, and so it should not be too surprising to find similar groups of ornithischians in the faunas of the Northern and Southern Hemisphere even after the final separation of the continents of Laurasia and Gondwana at the Middle-Late Jurassic boundary.

Early Jurassic saurischians from Gondwana are also indicative of a global Pangean dinosaur fauna at that time (see also Smith *et al.* 2007b). In theropods, coelophysoids are found on all major landmasses from which theropods have been reported (Raath 1969, 1977, Rowe 1989, Carrano and Sampson 2004, Irmis 2004, Tykoski 2005), with the exception of Antarctica. Furthermore, the recently recognized dilophosaur clade (Smith *et al.* 2007a, b) also shows a global distribution, with representatives known from

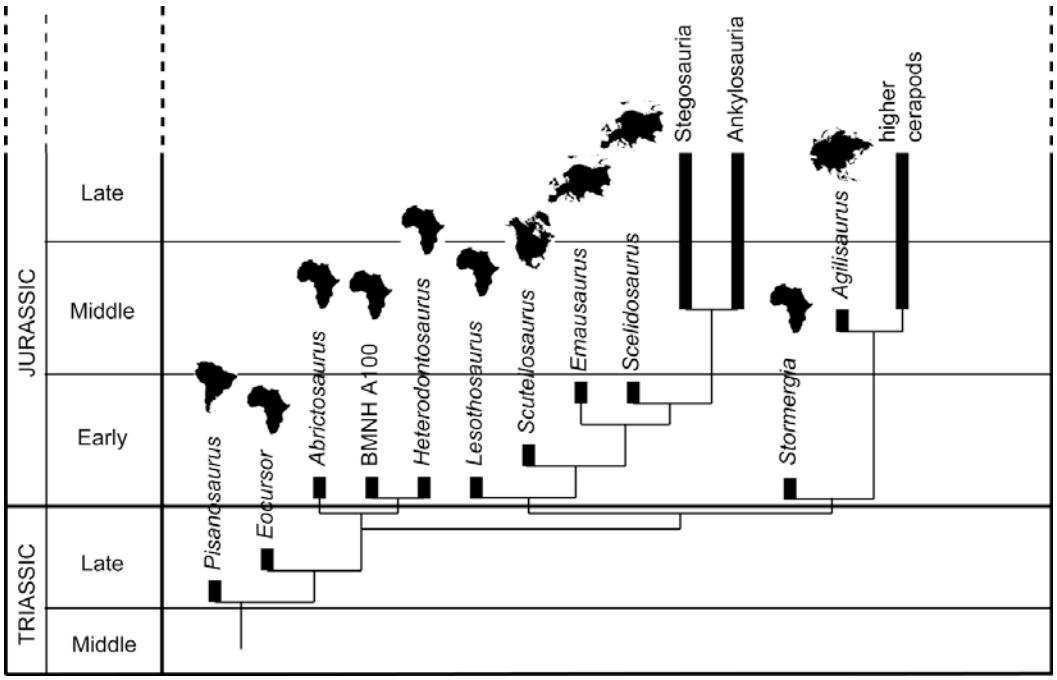

Figure 12: Phylogeny of early ornitischians (based on Butler *et al.* 2007, 2008), showing the geographic distribution of early ornitischians.

North America, China, South Africa, and Antarctica. Likewise, close relatives of the southern African sauropodomorph *Massospondylus* are known from the Early Jurassic of North (Attridge *et al.* 1985) and South America (Martínez 1999), and Smith and Pol (2007) found close relationships of this genus with the Chinese *Lufengosaurus* and the Antarctic *Glacialisaurus,* so that the Massospondylidae (*sensu* Smith and Pol 2007) represent another successful Pangean radiation of dinosaurs in the early Mesozoic. Thus, especially if the radiation of dinosaurs really followed a Late Triassic extinction event, as argued by Olsen *et al.* (2002), this Pangean distribution of many groups already in the Early Jurassic indicates high evolutionary dynamics and great dispersal potential of these animals. It might be noted, however, that high dinosaur diversity already in the Triassic in other parts of the world, including South America, and inferred ghost lineages argue against such a sudden radiation after a major extinction event at the T-J boundary.

Interesting is the report of a probable abelisauroid from the Early Jurassic of Gondwana (Allain *et al.* 2007). This lineage is almost entirely restricted to the Southern Hemisphere in the Late Jurassic and Cretaceous (see Tykoski and Rowe 2004, Rauhut 2005b), so its occurrence already in the Early Jurassic would represent a surprising case of endemism of this group, especially considering the northern Gondwanan (and thus more or less central Pangean) position of this find and the global distribution of most other groups.

Of special interest are furthermore the sauropods, which originated in the Triassic (see Yates and Kitching 2003), but seem to have experienced their first important radiation across the Triassic-Jurassic boundary. Gillette (2003: 686) suggested that Early Jurassic sauropods had a distribution in eastern Gondwana and southern and eastern Laurasia, and were restricted to middle latitudes, and that sauropods reached North America and western Gondwana only in the Middle or even Late Jurassic. Most of this argument was based on negative evidence, i.e. the lack of sauropod fossils from these regions during the Early Jurassic. Although some non-eusauropodan taxa were included in Gillette's analysis (*e.g. Vulcanodon*), most of this scenario invoves eusauropods, and, given the current confusion about the definition of Sauropoda, the following discussion will mainly consider Eusauropoda. New discoveries and paleogeographic considerations contradict the idea of restricted Early Jurassic faunas and an only Middle to Late Jurassic global distribution of sauropods. First, the discovery of probable sauropod remains in Antarctica (Smith and Pol 2007) might show that sauropods had reached low southern latitudes by that time, although a detailed study of this material is needed to establish its sauropod affinities and answer the question whether this material represents a basal taxon, or a eusauropod. Furthermore, the occurrence of *Amygdalodon* at around the Early-Middle Jurassic boundary in Argentina (Rauhut 2003b) and other fragmentary eusauropod remains from the Aalenian of this country (Salgado and Gasparini 2004) indicate that eusauropods were also present in western Gondwana early in the Jurassic. Considering palaeogeographic reconstructions of the Early Jurassic (Scotese 1991, Smith *et al.* 1994), it seems furthermore unlikely that a dispersal of eusauropods from eastern Gondwana to eastern Laurasia (*or vice versa*) could have happened withouth these animals entering North America as well. Indeed, the pre-

sence of *Anchisaurus*, which, according to Yates (2004), represents an early, non-eusauropodan sauropod (see also Fedak and Galton 2007), in the Early Jurassic of North America indicates that immediate eusauropodan outgroups already had a global distribution during this time. This is also in agreement with the find of the probable primitve eusauropod *Ohmdenosaurus* in central Europe (Wild 1978), a region that was geographically close to the eastern coast of North America. The absence of eusauropods from western North America might thus have pelaeoecological reasons, or might simply be due to incomplete sampling of these faunas. Thus, it seems most probable that eusauropods also reached a Pangean distribution already in the Early Jurassic.

In the Middle Jurassic, the change in theropod faunas from coelophysoid/basal theropod dominated Early Jurassic faunas to basal tetanuran faunas seems to have been paralleled in the Southern Hemisphere (Rauhut 2005a), though the timing and mode of this change remains uncertain due to the very poor Middle Jurassic theropod record of Gondwana, which, in terms of identifiable taxa, is restricted to the Cañadón Asfalto Formation. Basal, non-neosauropodan eusauropods were widely distributed in Gondwana during the Middle Jurassic, and seem to represent several lineages of an early radiation of eusauropods, some of which might go back to the early Jurassic. This notion is supported by the association of archaic forms in the later Middle Jurassic, such as *Archaeodontosaurus* (Buffetaut 2005) or *Volkheimeria* (Bonaparte 1986b, 1999), with much more progressive forms of sauropods, some of them already close to or within Neosauropoda, such as *Atlasaurus* (Monbaron *et al.* 1999, Upchurch *et al.* 2004). *Lapparentosaurus* is a taxon of problematic position, since it shows a combination of plesiomorphic and apomorphic characters (Upchurch *et al.* 2004). Upchurch (1998) found this taxon to represent a brachiosaurid, which would be the oldest record of a derived neosauropod, and argued that the primitive character of the vertebrae might be due to the juvenile state of the type material. However, the latter notion seems to be unlikely, since similar sized, juvenile specimens referred to *Patagosaurus* (MACN Ch 932, 934), for example, already show more complicated vertebral structures (OR pers. obs.). Thus, the phylogenetic position of this interesting taxon has to remain unresolved, pending a revision of the known, or the discovery of new material. Being intercalated within Laurasian taxa, or having close relatives in Laurasia, these Middle Jurassic sauropods furthermore indicate a generally Pangean sauropod fauna in the late Middle Jurassic.

Of special interest are, of course, the dinosaur faunas of the Late Jurassic of the Southern Hemisphere, since it is in these faunas that we would expect to find first consequences of the separation of Gondwana from the continents of the Northern Hemisphere. However, analysis of these effects has been hampered by the fact that, until very recently, only one dinosaur fauna had been reported from this period in Gondwana, that of the Tendaguru Beds in Tanzania, so that material for comparisons was missing (see above). This had another effect in the description of the fauna from Tendaguru: due to the lack of comparable material from the Southern Hemisphere, the taxa from this locality have generally been compared and often even been referred to taxa known from the Northern Hemisphere, which led to the emphasis on faunal similarities between the fauna of Tendaguru and especially that of the Morrison Formation. However, although this similarity certainly exists on higher taxonomic level, this might not be too significant, since most lineages represented probably reach back to the Middle Jurassic and thus to the time before the separation of Gondwana (see Remes and Rauhut 2005, Remes 2006, 2007). Recent work has furthermore shown that taxonomic assignment to Laurasian forms on lower taxonomic level is often questionable (Remes 2006), and the same is true for those forms still kept in the same genera as comparable taxa from the Morrison Formation. In the case of *Brachiosaurus brancai*, for example, a rigorous phylogenetic analysis of the taxa referred to the family Brachiosauridae would be necessary to test whether this species really is more closely related to *Brachiosaurus altithorax* from the Morrison Formation, or whether the latter might rather group with other Laurasian brachiosaurids, such as *Sauroposeidon*. The same is true for *Dysalotosaurus lettowvorbecki* (currently kept in the North American genus *Dryosaurus*, see Galton 1977, Norman 2004). In this case, the problem is even more acute, since *Dysalotosaurus* and *Dryosaurus* represent the only well-known dryosaurids, wheras all other taxa within the Dryosauridae are based on isolated elements or very fragmentary remains. Thus, no analysis of the interrelationships of dryosaurids has ever been attempted. In the case of *Elaphrosaurus*, the North American specimens referred to this taxon (Galton 1982, Chure 2001) might represent ceratosaurs, but cannot be referred to this genus (Rauhut and Carrano in prep). These examples again highlight the need for rigorous phylogenetic analyses as the basis for biogeographic interpretations, as already emphasized by Forster (1999).

In the absence of such phylogenetic analyses for the taxa concerned, a faunistic approach might shed some light on the biogeographic affinities of the Tendaguru fauna. Although similar in terms of taxonomic composition at higher taxonomic levels, the relative abundance of taxa and overall composition of the fauna from this locality is strikingly different from that of the Morrison Formation. In the latter, the most common sauropod is *Camarasaurus,* with its several species, and diplodocids, whereas titanosauriforms (only known from brachiosaurids in this formation) are very rare (Dodson *et al.* 1980, Foster 2003). In Tendaguru, in contrast, brachiosaurids and other basal titanosauriforms are among the most common sauropods (Russell *et al.* 1980),

which would be in good accordance with the titanosauriform dominated Cretaceous faunas in Gondwana. Although this difference might be assigned to palaeoecological reasons, the same seems to be true for the Kadsi Formation of Zimbabwe (Raath and McIntosh 1987) and, maybe, the Cañadón Calcáreo Formation of Argentina (with *Tehuelchesaurus* representing a basal titanosauriform or an immediate titanosauriform outgroup, Rauhut *et al.* 2005, Carballido *et al.* 2007), though more sampling is needed to confirm this. In the latter case, the paleoecological setting seems to be different from that of Tendaguru, and this locality was placed considerably further south than the latter in Late Jurassic times.

In addition to this relative abundance of specimens, differences in the faunal composition are also reflected in the taxonomic composition of the sauropod faunas (Fig. 13). For this comparison, only the sauropod fauna of the Morrison Formation (Foster 2003, Upchurch *et al.* 2004) and the Late Jurassic of Portugal (Antunes and Mateus 2003) have been considered for the Northern Hemisphere, since eastern Asia was separated from western Laurasia and Gondwana by epicontinental seas from at least the Bathonian (Smith *et al.* 1994), and, thus, the Chinese Late Jurassic sauropod fauna shows a rather high endemism and can thus not be regarded as a "typical Laurasian" fauna (Upchurch *et al.* 2002). For the Southern Hemisphere, the Tendaguru fauna and the two named taxa from the Cañadón Calcáreo Formation have been considered together as representatives of the Late Jurassic Gondwanan fauna. Taxa have been counted on species level.

Looking thus at sauropod faunal composition, diplodocids constitute more than half of the known sauropod taxa from the Northern Hemisphere (11 of 21 species), whereas basal titanosauriforms (2 species) account for only ten percent of the species. Camarasurids are the second most important faunal element, with 14% (3 species). In contrast, basal titanosauriforms (or immediate titanosauriform outgroups) account for almost half of the species in the Southern Hemisphere (4 of 9 species), followed by dicraeosaurids (3 of 9 species), whereas only two species of diplodocids have been described from Gondwana. The most remarkable aspect of this faunal comparison, however, is the lack of one of the most common groups of sauropods from the Morrison Formation, the camarasaurids, in Gondwana, and, in turn, the lack of an important Gondwanan lineage, the dicraeosaurids, in Laurasia. Although the former might still be accounted for by the poor Gondwanan fossil record and the very different sample sizes, the latter is especially noteworthy, since dicraeosaurids have been reported from all three Gondwanan localities that have yielded identifiable Late Jurassic sauropods (Raath and McIntosh 1987, Aberhan *et al.* 2002, Rauhut *et al.* 2005), even though they are geographically, latitudinally (and thus probably climatically) and, as far as can be said at the current state of knowledge, ecologically disparate. Since the phylogenetic relationships of both camarasaurids and dicraeosaurids indicate that these groups must have originated in Pangean times as well, their absence in the Late Jurassic in one of the Hemispheres must either be due to the failure to disperse to the other Hemisphere in Middle Jurassic times, or to differential extinction in Laurasia and Gondwana (see also Harris and Dodson 2004). Although this question can only be answered by new discoveries, the lack of these important faunal components in the respective other Hemisphere might thus represent a first sign of differential evolution of the dinosaur faunas of the two Hemispheres due to limitations in dispersal potential, following the separation of Gondwana.

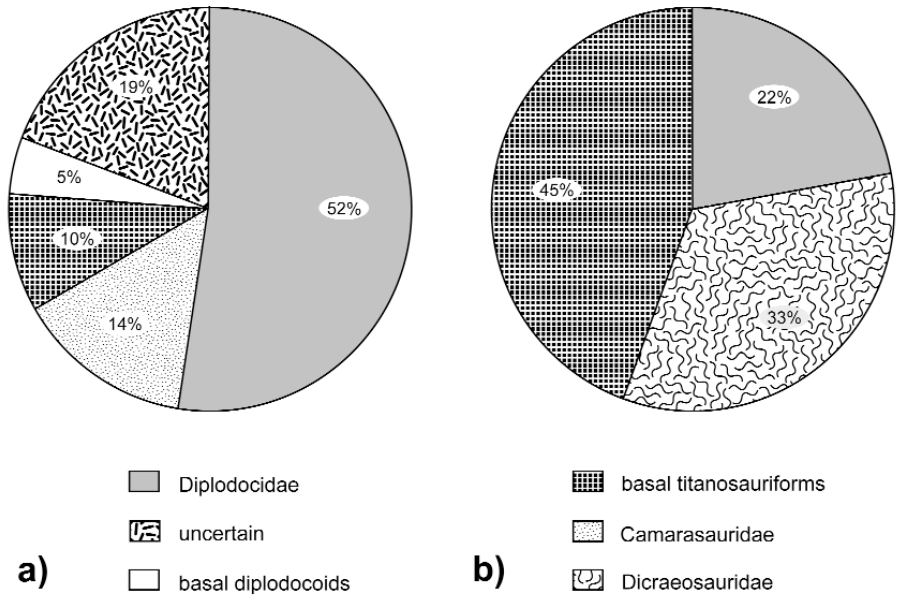

Figure 12: Taxonomic composition of Late Jurassic sauropod faunas of the Northern and Southern Hemisphere. a) Taxa represented in the Morrison Formation, USA and various localities in Portugal. b) Taxa represented in the Tendaguru Beds, Tanzania, and other Gondwanan localities. Basal titanosauriforms in b) include Tehuelchesaurus, which might be an immediate titanosauriform outgroup.

CONCLUSIONS

Jurassic archosaurs from the Southern Hemisphere are still rather poorly known. Although this is especially true for terrestrial crocodiles and pterosaurs, the dinosaur record from Gondwana is also still far from complete. The most important archosaur faunas from the Jurassic of the

Southern Hemisphere are that of the Hettangian-Sinemurian Elliot and Sinemurian-Pliensbachian Clarens formations of southern Africa, the (?) Hettangian-Toarcian Kota Formation of India, the Early Jurassic Hanson Formation of Antarctica, the Callovian Cañadón Asfalto Formation of Argentina, and the Kimmeridgian-Tithonian Saurian Beds of Tendaguru, Tanzania. Marine crocodiles are especially well-represented in the western part of southern South America, from where different taxa are known from units ranging from the Sinemurian to the Tithonian. Multiple events of faunal exchange through the sporadically open Hispanic corridor during the Early and Middle Jurassic might have been an important factor in thalattosuchian evolution.

Terrestrial archosaur faunas show a Pangean distribution in the Early Jurassic, and, most probably in the Middle Jurassic (for which almost no terrestrial crocodiles have been reported from the Southern Hemisphere). The rather high diversity of basal ornithischian dinosaurs in the Early Jurassic of southern Africa might indicate that the early radiation of this clade took place in southern Gondwana. In the Late Jurassic, especially sauropod faunas might already show the first indications of differential faunal evolution between the Southern and Northern Hemisphere.

However, given the patchy archosaur record from the Jurassic of Gondwana, all current interpretations of archosaur evolution and faunal differentiation during this epoch must be seen as tentative. More material is needed, especially from the Southern Hemisphere, to better understand archosaur evolution, in particular the effects that the initial continental breakup during the Jurassic might have had on the evolutionary history of this group.

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